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

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Date: June 15 / 2023

Thabang Rainett Teffo

Signature

DEDICATION

In loving memory of my beloved mother, Maphuti Betty Teffo. You will forever be in my heart.

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List of acronyms and codes

IUCN – International Union for Conservation of Nature

PAs – Protected Areas

UAS – Unmanned Aircraft Systems

UAVs – Unmanned Aircraft Vehicles

EU – European Union

LC – Least Concern

VU – Vulnerable

EN – Endangered

UN – United Nations

USA – United States of America

eDNA – environmental DNA

m – meter

mm – millimeter

ha – hectare

1. BACKGROUND OF THE WORK AND ITS AIMS

1.1. Study background

An important element of Earth's terrestrial ecosystems is the population of wild ungulates, which is made up of a wide variety of hooved animals. They include antelopes, deer, and wildebeests, etc, they graze across several continents and help maintain balance of nature. Wild ungulates in the world are expected to be in the hundreds of millions as of the most recent statistics up to 2021, with each species having specific difficulties with conservation (IUCN, 2022). In addition to altering plant communities and ecosystems, this population dynamic also acts as prey for a variety of predators. It is evident that populations of several herbivorous or omnivorous large ungulate species (such as red deer or wild boar) are increasing globally. This is mainly due to reintroduction processes, absence of apex predators and good adaptation to human-transformed fewer natural habitats (Côté et al. 2004; Ramirez et al. 2018). Hence in the northern hemisphere much more research efforts have ventured into understanding ungulate population dynamics and management (Larter et al. 2000).

Ungulate herbivory can have significant top-down effects on the density and composition of plant communities in an ecosystem (Carpio et al. 2015; Rhodes and St. Clair, 2018). According to Katona and Coetsee (2019) ungulates may also have direct and indirect impacts on faunal diversity, using reptiles as an example, ungulates such as wild boar can directly feed on them (causing a negative impact). Some of the indirect impacts caused by deer and wild boar may include, changing vegetation dynamics, resulting in limitations, or improvement of the available habitats.

The world ecosystems continuously experience tremendous reduction of reptile species (Carranza et al. 2018; Miranda and P, 2017). While reptiles represent world's most diverse populations of terrestrial vertebrates and are a major component of the global biodiversity, they are significantly important for their key role in ecology and from evolutionary point of view (Pincheira-Donoso et al. 2013). Change in the landscape due to fragmentation has a direct impact resulting in habitat loss in reptile communities. Wherein populations of reptiles are found in humandominated landscapes (i.e., urban areas). Highly fragmented habitats result in the establishment of subpopulations leading to reduced genetic diversity and local extinctions (Dixo et al. 2009).

However, ungulates may be considered ecosystem engineers in areas where they live (Baruzzi and Krofel, 2017), in areas where snakes and other reptiles co-habit, may also result in a negative impact (McCauley et al. 2006). Ungulate occurrence in an ecosystem may alter the habitats by modifying vegetation cover, soil and water properties, through activities such as rooting, urinating, grazing and trampling. These activities may gradually alter reptile habitats (breeding, hibernating and feeding sites) and change their behavioral patterns (Heigl et al. 2017) including their movements.

Like ungulates, the human population has accelerated enormously with subsequent increase in demand for space use, resources and rapid development of infrastructure (Ciuti et al. 2012), including but not limited to recreational areas. The Frequent appearance of humans in the area harboring wild fauna may result in direct and indirect interactions, which are mostly found to be negative (Xu et al. 2021). The negative impacts of anthropogenic proximity to wild populations include alteration of behavior (Wilson et al. 2020), i.e., daily activities, limited and reduced movements (Yackulic et al. 2011) which ultimately hinders their ability to forage, hunt, find mating partners, etc.

1.2. Research problem

1.2.1. Increase of ungulate populations

Understanding the population dynamics of ungulates is significantly critical given their ecological and economic importance (Paterson et al. 2019). Recently the world ecosystems have been experiencing a significant increase in the population of ungulates in numbers and their geographic range sizes, especially in the northern hemisphere (Apollonio et al. 2010). The increase in ungulate communities is closely related to human socio-demographic modifications in addition to the availability of unused lands and indigenous agricultural practices, which results in an abundant food supply for ungulates (Valente et al. 2020). Lack of native predators (Skogland, 1991), strict hunting legislation and declining numbers and increasing age of hunters (Carpio et al. 2017) may also play a significant role in the current increasing population of ungulates.

Recently ungulates have increased tremendously in numbers and geographic range size across Europe (Valente et al. 2020). In other regions including Europe and North America, studies have recorded a great expansion of ungulate population size with extended geographic ranges (Nichols et al. 2015). Such changes may cause tremendous ecological dynamics in the landscape (Côté et al. 2004). Hungary harbors five species of free-living population of ungulates; red deer (*Cervus elaphus*), fallow deer (*Dama dama*), European mouflon (*Ovis aries musimon*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) (Csányi and Lehoczki, 2010), which are found in different type of habitats; natural (forests), semi-natural and urban habitats (agricultural areas and urban cities human-dominated landscapes). In our study area the most important ungulate is the wild boar. However, there are also populations of deer species in the study area.

1.2.2. Decrease and vulnerability of reptile populations

While populations of reptiles are significantly declining across the world (Gibbons et al. 2000), many snake species are threatened by extinction. In Hungary, there are 15 different reptile species, all of them which are protected by law (www.herpterkep.mme.hu last accessed 15 March 2023). However, studies on their actual ecological status and the threatening factors are relatively scarce. In this study we will focus on a snake species, the Caspian whipsnake (*Dolichophis caspius*). Caspian whipsnake is a large-bodied (reaching and occasionally exceeding 2 meters in total length) colubrid with a distribution area covering south-eastern Europe, including the Balkans and the steppe region extending eastward between the Black and the Caspian Seas (Dyugmedzhiev et al. 2019; Sahlean et al. 2019). The north-western edge of its distribution reaches North-Central Hungary (Nagy et al. 2010). In the Carpathian Basin, the distribution of the Caspian whipsnake populations has become increasingly disconnected owing to habitat fragmentation (Mahtani-Williams et al. 2020). The species inhabits dry steppe and Mediterranean habitats (Bellaagh et al. 2008).

According to the IUCN Redlist, Caspian whipsnake is in the least concern category, based on its status in the entire native range. In Hungary the species exists in small, isolated populations: i.e., in southern Hungary (Szársomlyó Hill), along the western bank of the Danube River and on dolomite, limestone and sandstone outcrops in and around Budapest (Nagy et al. 2010), wherein the area is under pressure of shrub encroachment. The Caspian whipsnake is strictly protected in Hungary, threats to this species are not thoroughly studied, but habitat loss and road traffic (https://herpterkep.mme.hu/) are considered as primary threats to its survival. Additionally direct observations have revealed the presence of humans associated with recreational activities in the study area. The presence of humans in this area may also pose a significant threat to the Caspian whipsnake population either directly or indirectly.

Albeit the existing broad literature on the impacts of ungulates on wildlife and habitats, the impacts which wild ungulates have on reptiles and their habitats at large are still significantly unknown. While at the same time, impacts on Caspian whipsnake have never been studied before. This research study focuses on the impacts of ungulates in the peri-urban habitat of the Caspian whipsnake. We investigated if wild boar rooting activity may influence the shrub encroachment process and if ungulate browsing pressure may have any impact on the composition of the cover of woody vegetation. Given the spatial ecology of the Caspian whipsnake in the region in relation to the many habitat patches, it is clear that effective conservation management and ecosystem preservation depend on a thorough understanding of its movement patterns and resource use.

1.3. Rationale

1.3.1. Ungulates impact on reptiles

Ungulate activities and behavior; such as wild boar 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 (Sandom and Hughes, 2013), 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). Snakes are significantly important vertebrates in the trophic chain. Frequent or effective predation (e.g., by wild boar) in an ecosystem may suppress and cause decline in the populations of snakes and other reptiles (de Schaetzen et al.

2018). 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).

1.3.2 Ungulate impact on Caspian whipsnake populations in Hungary

Naturally occurring reptile populations are tremendously decreasing worldwide (Gibbons et al. 2000), in the mist of this some snake species are threatened by extinction. Studies on the ecology and factors threatening reptile's species are seldom. The Caspian whipsnake 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.

1.4. Aim of the study

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.

1.4.1. Research objectives and questions

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?

1.4.2 Hypotheses

In terms of the general impacts of ungulates on reptile species around the World, we hypothesized: **Ha** – 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: **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. **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, **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 impacts.

2. LITERATURE REVIEW

This chapter outlines an overview of the potential direct and indirect impacts of ungulates on reptiles (ungulate-reptile interactions). It highlights the state of ungulates and reptile populations in Europe, ungulates activities and the impacts they exert on habitats and reptiles (squamates) including different types of landscapes inhabited by both ungulates and reptiles. Furthermore, the chapter elaborates on the technical methods of monitoring of vegetation composition and reptile species. Additionally, analytical methods which can be used for the analysis of spatial ecology and vegetation data are discussed.

2.1.Ungulate populations, trends and their effects.

Ungulate population dynamics mirror sophisticated interactions between abiotic and biotic factors including differences in environmental conditions, predation rates and harvests (Gaillard et al. 2000; Paterson et al. 2019). It is important to understand the influence of each of these factors on the ever-changing populations, given the paramount role ungulates have in ecosystems (Gordon et al. 2004).

Large ungulates play a pivotal role. Firstly, in the economies, they generate revenue through recreational hunting and ecotourism (Leader-Williams et al. 2001; Ogutu, 2002; Van Der Waal and Dekker, 2000), for example in the event of hunting in the United States of America (USA), it has been confirmed that recreational value of hunting may range between 13 and 545 USD/hunting day (Gren et al. 2018). Secondly, some ungulates are prioritized for conservation purposes, most of these species are encountering threats of habitat loss, overhunting and human persecution. Globally, approximately, 48% (n = 84) of ungulates species are either flagged as critically endangered, endangered or vulnerable in the *Red list Data Book* of the IUCN. Some ungulate species are regarded as indicators for conservation and management planning because of their role in ecosystems and because they are keystone species (Gill, 2006). And finally, ungulates (wild and livestock) or herbivores in particular, are responsible for grazing, which ultimately have an impact on the composition and structure of the vegetation and functioning of ecosystems (Balakrishnan et al. 2014; Roberts et al. 2021).

Similarly, Hungary has been observing a tremendous increase in ungulate (i.e., deer species) populations (Csányi and Lehoczki 2010). These increases in deer populations (red deer, roe deer, and fallow deer have a significant impact on the forested and agricultural areas across the country (Cote et al. 2004). Selective grazing and browsing by ungulates may result in the modification of plant diversity in forests and tend to induce interspecific competition between herbivores. However, with the availability of adequate abiotic environmental conditions, such as suitable temperature and moisture, trees and/or plant communities can survive impacts of browsing exerted on them by ungulates. Therefore, species-specific ungulate browsing may potentially contribute in shaping woody species distribution and composition.

Although the dense populations of ungulates may bring financial benefits for conservation and society through tourism and hunting (Weisberg et al. 2002), ungulates with high reproductive capabilities (Servanty et al. 2011) may exert significant impacts on other wildlife species in an ecosystem. Different ungulate species can follow different foraging strategies and feed on diverse food items (Miranda et al. 2012), *e.g.*, they may graze, browse or do both; furthermore, when feeding they prefer certain habitat patches, plant species and plant parts and feed at specific heights within the available vegetation strata (Nichols et al. 2015). Consequently, their various feeding behavior (including selective feeding, trampling and defecating) generates diverse changes in the vegetation patterns and animal communities of the habitats (Howland et al. 2016; Nasseri et al. 2011).

Despite the ever-changing climatic conditions affecting biodiversity across the globe, some ungulate populations are thriving and gaining stability (i.e., wild boar, red deer and wildebeests (*Connochaetes spp.*) (Homewood et al. 2001; Ruiz-Fons, 2017). Similar trends of population increase in ungulate species are observed in Europe, wherein they become overabundant in some regions (Valente et al. 2020). Such tremendous increase is prompted by factors such as strict hunting legislations, abandonment of land, rewilding and re-naturalization of habitats, reduced number of hunters and lack of natural predators in some regions; for example, the disappearance of the wolf (*Canis lupus*) in the Iberian Peninsula (Bosch et al. 2012; Mesinger and Ocieczek, 2021; Ordiz et al. 2022).

2.2. Methods used to measure ungulate impacts

Various methods may be utilized to measure and monitor the impacts of ungulates on vegetation. With the development of new technologies, recent methods range from traditional technical field observations, e.g., quadrats count to more complex methods which include DNA analysis and the use of Unmanned Aircraft Vehicles (UAVs, i.e., drone technology).

2.2.1. Measuring ungulate browsing and grazing.

When it comes to impacts on forest herbaceous plant communities, it is evident that ungulates may have a tragic effect on biodiversity by reducing the herb layer cover and richness (Russell et al. 2001; Stockton et al. 2005). Although, previous studies have shown that ungulate browsing pressure may offset the shrub encroachment process and/or succession (Pápay et al. 2020). In areas where moose (*Alces alces*), roe deer, fallow deer, and red deer can co-exist (i.e., Europe and North America), it is often tedious to determine by which species the type of impact is contributed. However, certain characteristics of foraging behavior may be distinguished between some species; i.e., moose and roe deer are known to browse extensively whereas red deer and fallow deer are mixed feeders, but fallow deer are known to fall closer to the grazer end of the continuum (Hofmann, 1989). Although studies focus mainly on measuring the impact of the entire ungulate communities in the ecosystem, some may tend to direct their focus to a specific species within a particular habitat. Such methods by which foraging selection of a single ungulate species on the vegetation is studied using control feeding trials are also known as "*cafeteria tests*" (Averill et al. 2016).

Other studies have gone beyond measuring impact to the extent of understanding forest regeneration by measuring the impacts of ungulates on saplings (Hejel et al. 2016) rather than the actual adult vegetation. In literature, browsing impact by ungulates may also be measured using selectivity indices; for example Katona et al. (2013) conducted a habitat-based study (forest) focusing on how ungulate browsing and climate change may have an impact on forest habitat. From this work, it was found that browsing can be highly selective and may have the potential to reduce the occurrence of some preferred species in the forests.

Increases in ungulate populations may result in changes in the vegetation structure and ultimately change the plant species richness in an ecosystem (Vild et al. 2017). These types of changes may be difficult to predict, more so in multi-species ecosystems containing various ungulate species with different feeding preferences and foraging behavior. These relationships between plant communities and herbivores are of paramount significance and may aid in understanding trophic interactions, reintroductions and invasions by certain species. Thus, it is of the utmost importance to understand which plant species ungulates like and how these preferences can influence their succession.

To study the dietary relationship between ungulates and plant communities' scientists use feeding trials, also known as cafeteria tests, by simultaneously providing different kinds of feeds, plant species, or plant materials and observing the selection of the animal among them. Such a study may reveal which plant species are preferred over others by certain ungulates. Like any other methodology there are limitations and/or disadvantages (Renaud et al. 2003). In such areas ungulate bites may appear similar and data collection through direct observations of the animals' choices can be time-consuming or close to impossible to conduct. Hence, most feeding trials research is conducted with ungulates in captive areas.

DNA technology provides a solution to study cryptic behavior in animals, including herbivory. Several tools are developed to investigate the extent of ungulate browsing based on their foraging behavior; by chewing on shrubs, browsing on buds and leaves or branches of trees, animals always leave DNA evidence (saliva and environmental DNA) in the forests which may be used for species identification (Nichols et al. 2015; Nichols and Spong, 2014).

Advantages related to this methodology include a high potential for reliability and further regarded as time-efficient approach, which may contribute highly to herbivore-plant interactions (Kudoh et al. 2020). The use of DNA technology is applied across all herbivores ranging from small herbivores to large ones, including ungulates (i.e., deer species) (Garnick et al. 2018; Soininen et al. 2009).

2.2.1.1. Exclusion experiments.

Herbivory plays an important role in altering and restructuring vegetation communities (Maron and Crone, 2006), not only in forest habitats but also in arid savannas. Different behaviors in feeding and vegetation preference by browsers have a major impact on some of the savanna biomes, mainly in South Africa and West African savanna woody vegetation communities (Wigley et al. 2014).

The use of existing long-term exclosures in African protected areas (Fig. 1.) may provide a perfect opportunity to thoroughly distinguish the role of browsing animals in modifying woody species composition.

Figure 1: Differences in vegetation richness in exclusion experiment: (A) Full exclosure and (B) partial exclosure on a low-productivity site in the Satara region of Kruger National Park (see; Burkepile et al. 2017).

Studies have proved that there exist taller canopies and higher tree and shrub densities within enclosures in most protected areas in African savannas (Asner et al. 2009; Levick et al. 2010). In temperate rainforests (i.e., North America and Europe) long term studies on ungulate impact using enclosure methods are prevalent (François et al. 2013; Woodward et al. 2021), additionally in Europe similar methods were tested and coupled with the use of fire, wherein it was found that burning had an impact on regeneration of certain woody species (Petersson et al. 2020).

2.2.2. Estimating the effects of wild boar rooting.

In Europe, wild boar is a native forest-dwelling species. Wild boar populations have been increasing since the 19th century. Within Europe their populations have been exponentially increasing in their distribution range (Csókás et al. 2020). As a result, they are considered a pest in various areas in and outside of their geographic range. Wild boar is unique compared to other terrestrial pest species as they are largely omnivorous generalists and are considered both large predators and herbivores in their native and non-native range (Barrios-Garcia and Ballari, 2012).

Their foraging is mostly extensive disturbances which include turning over of the top layer of the soil while searching for food underground including but not limited to earthworms and plant roots. This type of disturbance is largely known as ‘rooting’. This process may affect various ecosystem components either directly or indirectly. The impact is made directly on the soil and indirectly on the vegetation/plant composition in the ecosystem (Hone, 2002).

Sensitive habitats such as the Pyrenean alpine grasslands may be threatened by rooting activities. Therefore, investigating the direct and indirect impacts of wild boar rooting is significantly important in ecology. Albeit, the difficulty in quantification of wild boar rooting in the northern hemisphere, several methods (i.e., drones, quadrants and/or transects) are used to determine such impacts of rooting on animals and plant communities (Gray et al. 2020). There are various tools to evaluate the impacts, this includes geographical positioning systems and transects. In some instances, direct observations and/or estimations are still used (Sütő et al. 2020).

2.2.2.1. Using drone technology to measure wild boar rootings.

There is an increasing interest in research to use drone technology as a tool in wildlife ecology. The technology has become cost-effective (Linchant et al. 2015). Recently technology has been at the forefront of solving scientific problems. One of the sectors in which technology is used to help solve these problems is environmental monitoring (Koh and Wich, 2012). This includes investigating damages that may be caused by wild boar rootings in forest, urban and agricultural areas.

The prevalence of wild boar in the northern regions is mainly linked to damage to agriculture (Rutten et al. 2018). Although it is difficult to measure the amount of damage and impact caused by wild boar rooting, recently using UAS(i.e., drones) to estimate and/or measure the degree of disturbance has become very popular. Drones have proven to be more accurate in estimating the amount of disturbance in grasslands than in agricultural fields and forests; i.e., in a study by Rutten et al. (2018), it was found that the accuracy of the estimates on damage caused by wild boar in maize fields (agricultural area) was 84% while accuracy in grasslands was 94%. Although when compared to traditional ground-based methods of damage estimation, it was found that UAS methods tend to underestimate the damaged areas. But UAS are more effective while traditional ground-based methods are time-consuming and labor-intensive(Michez et al. 2016).

2.2.3. Monitoring ungulates using camera traps.

The rapid development of technology gives opportunities for researchers to utilize modern techniques which aid in closely monitor wild animals with less interference (Neuharth et al. 2020). Monitoring biodiversity on a small and large scale could be a challenging activity (Kühl et al. 2020) for researchers; choosing the adequate method to observe and monitor animal species could be a challenge, too (Gužvica et al. 2014). However, all these may depend on the habitat type and behavior of the species. Individual monitoring methods have been developed for marine animals, insects and terrestrial animals. Monitoring techniques such as camera trapping were traditionally used to monitor mostly mammals and birds (Welbourne et al. 2019).

Today camera-traps have become significantly useful tools for detecting the presence or absence of different animals ranging from illusive reptiles (snakes and squamates) to large mammals including ungulates. This camera-trapping technology is used for solving a range of research issues related to movement, distribution and ecology (Fleming et al. 2014; Torretta et al. 2017).

As ungulate populations increase, camera trapping has become a large data-capturing methodology; studies continue to adopt new methodologies such as the mark-resight method, in measuring the abundance of ungulates (Taylor et al. 2022). Such data is later quantified in estimating the damage or impact that may be caused by those ungulates in a particular habitat. Camera traps are also used to determine the spatio temporal overlap and interactions within similar and between different species (Zanni et al. 2021), integration of methodology has proved to yield reliable results; i.e., in a study on ungulate foraging patterns (Rhodes et al. 2018) used a combination of camera-trapping and exclosure experiments to test for the impact of herbivory on aspen species post-fire activity.

2.3. Reptile populations and their threats.

Reptiles are one of the most ecologically and evolutionarily remarkable classes of living creatures, and have colonized nearly every part of the globe, including the seas and some of the world's most harsh and environmentally fragile environments (Pincheira-Donoso et al. 2013). Many reptile species share similar habitats with ungulates (Shine and Somaweera, 2019) mainly in terrestrial environments. Within the animal taxa reptiles face strong declines globally (Bland and Böhm, 2016), and their populations are tremendously fragmented (Meek, 2012).

Some species persist in smaller and increasingly fragmented geographic ranges (Nally and Brown, 2001; Subedi et al. 2022), wherein the most vulnerable species require active conservation measures to ensure their survival. For example, the Australian tiger snakes (*Notechis scuatus*) and the African rock pythons (*Python sebae*) endure limited space use and movements due to habitat fragmentation (Fahrig, 2003). Disturbances associated with urban areas such as fragmentation, invasive species, road accidents and isolation of refugia may result in mortality of sensitive species (Reed and Krysko, 2014; Subedi et al. 2022).

Factors related to the decrease in reptile species include but are not limited to human use of animals. Consumptive use and/or harvesting may be the main problems associated with reptiles' decline (Gibbons et al. 2000). Overconsumption is a problem for some snake species, for example, overharvesting of ocellated mountain viper (*Vipera wagneri*).

There are 15 species of reptiles in Hungary (www.anamialia.bio, last accessed 13 May 2023). Four of these are from the family Colubridae family (*Natrix natrix, Zamenia longissimus, Natrix tessellata, Dolichophis caspius*), meaning about 30% of the reptiles are snake species. The

Hungarian meadow viper (*Vipera ursinii rakosiensis*) has a population status of vulnerable (VU) on the IUCN Red List and its population numbers are showing a decreasing trend. It is strictly protected in Hungary. The Caspian whipsnake is listed as Least Concern, however, in Hungary, this species is also strictly protected.

Most reptile populations are threatened by factors such as habitat destruction resulting from unsustainable and intensive agricultural practices (Tan et al. 2023). Most snake species suffer from pet collection for trade, and species may be greatly threatened with extinction should the trade not be halted or reduced (Hierink et al. 2020). Other important threats may include fires (Lazzari et al. 2022; Santos et al. 2022), land developments (construction) and/or land use changes, anthropogenic leisure activities ((including, running, jogging walking dogs and recreational visits) (Kuipers et al. 2021), afforestation and persecution by humans.

2.4. Movement ecology of snakes.

Knowledge about the spatial behavior of species living in human-dominated landscapes is insufficient (Dodd and Barichivich, 2007; Lepczyk et al. 2017; Todd and Nowakowski, 2021). It seems that in disturbed and fragmented habitats (including urban landscapes), snakes use smaller areas in general. For example, the colubrid Coachwhip (*Masticophis flagellum*) and the Eastern indigo snakes (*Drymarchon couperi*) maintain smaller home ranges than in natural habitats (Getz et al. 2007; Mitrovich et al. 2009). In undisturbed habitats, even large-bodied snakes may establish larger home ranges, as was observed in the Northern Pinesnakes (*Pituophis m. melanoleucus*) in the New Jersey pine barrens where large males covered over 258 ha (Graitson et al. 2019). Similarly, in a nature reserve in Southern Florida, the annual home range of the Eastern indigo snake was 110 ha for females and 207–233 ha for males (Worton, 1987).

Besides habitat quality, the variation of movements in snakes is also influenced by the combination of sex, season, and latitude (Brito, 2009; Metcalf et al. 2021). For instance, in the case of the temperate zone, Eastern indigo snake males establish larger home ranges and move longer distances than females (Bauder et al. 2016). Jellen et al (2007), showed that, during mating season the crotalid Eastern Massasuga (*Sistrurus catenatus*) males followed and mated with several females. As a result, males moved larger average daily distances (21.8 m) during the mating season as compared to non-mating season (13.3 m). In general reptiles in the temperate zones are mostly active during the warmer months and are inactive during winter and seldom move within their hibernacula (McEachern et al. 2015).

2.5. Ungulate-reptile interactions.

Ungulate species can follow different foraging strategies and feed on diverse food items, *e.g.,* they may graze, browse or do both (Teffo et al. 2023); furthermore, when feeding they prefer certain plant species and plant parts and feed at specific heights within the available vegetation strata (Katona et al. 2013). Consequently, their various feeding behavior (including selective feeding, trampling and defecating) generates diverse changes in the vegetation patterns and animal communities of the habitats (Howland et al. 2016; Nasseri et al. 2011).

Reptile species may be directly and indirectly impacted by the presence of dense populations of ungulates through grazing (by both livestock and wild ungulates), trampling and opportunistic predation (Katona and Coetsee, 2019).

High levels of ungulate disturbances can homogenize the areas and destroy favored habitat patches by reptiles (Kazmaier et al. 2001; Meek, 2012), however, preferential effects of ungulates can also establish appropriate habitat or foraging opportunities for reptile species (McCauley et al. 2006; Katona and Coetsee, 2019). On the other side, some large mega predatory reptiles (*e.g.,* Komodo dragon *(Varanus komodoensis*) may have a direct negative impact on ungulates but the lack of these ungulates as prey may be a significant threat to them (Kazmaier et al. 2001; Ariefiandy et al. 2013). Monitoring of ungulate populations and their effects in the ecosystems is crucial to mitigate the threats to herpetofauna and mainly enhance the beneficial outcomes from ungulate presence.

Despite the ever-changing climatic conditions affecting biodiversity across the globe some ungulates are thriving and gaining stable populations (*i.e.,* wild boar, red deer, wildebeest (*Connochaetes spp.*) or reindeer (*Rangifer tarandus*) (Homewood et al. 2001; Massei et al. 2015; Ruiz-Fons, 2017). Although the dense populations of ungulates may bring financial benefits for conservation and society through tourism and hunting, ungulates with high reproductive capabilities (Weisberg et al. 2002) may exert significant impacts on other wildlife species in an ecosystem. Different ungulate species can follow different foraging strategies and feed on diverse food items (Côté et al. 2004), *e.g.*, they may graze, browse or do both; furthermore, when feeding they prefer certain habitat patches (Ben-Shahar and Skinner, 1988, p.; Miranda et al. 2012; Servanty et al. 2011), plant species and plant parts and feed at specific heights within the available vegetation strata (Homolka, 1996). Consequently, their various feeding behavior (including selective feeding, trampling and defecating) generates diverse changes in the vegetation patterns and animal communities of the habitats (Nichols et al. 2015; Zweifel-Schielly et al. 2009).

Reptiles are one of the most ecologically and evolutionarily remarkable classes of living creatures, having colonized nearly every part of the globe, including the seas and some of the world's most harsh and environmentally fragile environments (Howland et al. 2016). Many reptile species share similar habitats with ungulates (Nasseri et al. 2011) mainly in terrestrial environments. Within the animal taxa, reptiles face strong declines globally (Pincheira-Donoso et al. 2013; Shine and Somaweera, 2019) and their populations are tremendously fragmented (Bland and Böhm, 2016). Reptile species may be directly and indirectly impacted by the presence of dense populations of ungulates through grazing (by both livestock and wild ungulates), trampling and opportunistic predation.

3. MATERIALS AND METHODS

This chapter explores an integrated methodological approach categorized into two parts 1) Broad Literature Survey (BLS) to describe the general effects of ungulates on reptiles in different continents, and 2) Technical Field-Based Research (TFR), to achieve the objectives and answer questions raised in chapter 1.4 of this thesis, the following methods are explored: A BLS investigating ungulate-reptile interactions at a global scale followed by a TFR focusing on shrub cover analysis in the study area using field data collection and drone technology, vegetation survey which includes shoot availability and browsing impact by ungulates (i.e., deer), measuring wild boar rooting patterns and the relationship with shrubs and saplings (with shrub encroachment), investigate the spatial ecology of Caspian Whipsnake using radio-telemetry, camera trapping methods to capture snake activity and presence of other animals in the study area (i.e., predators and/or other ungulates) including human presence.

3.1. Broad literature survey: ungulate-reptile interactions

3.1.1. Literature search and paper selection.

We performed a broad literature search on the Web of Science database (Clarivate; https://www.webofknowledge.com), in accordance withthe 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 thatwe 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.

3.2. Technical field-based research

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

3.2.1. 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 (Fig. 2). 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.

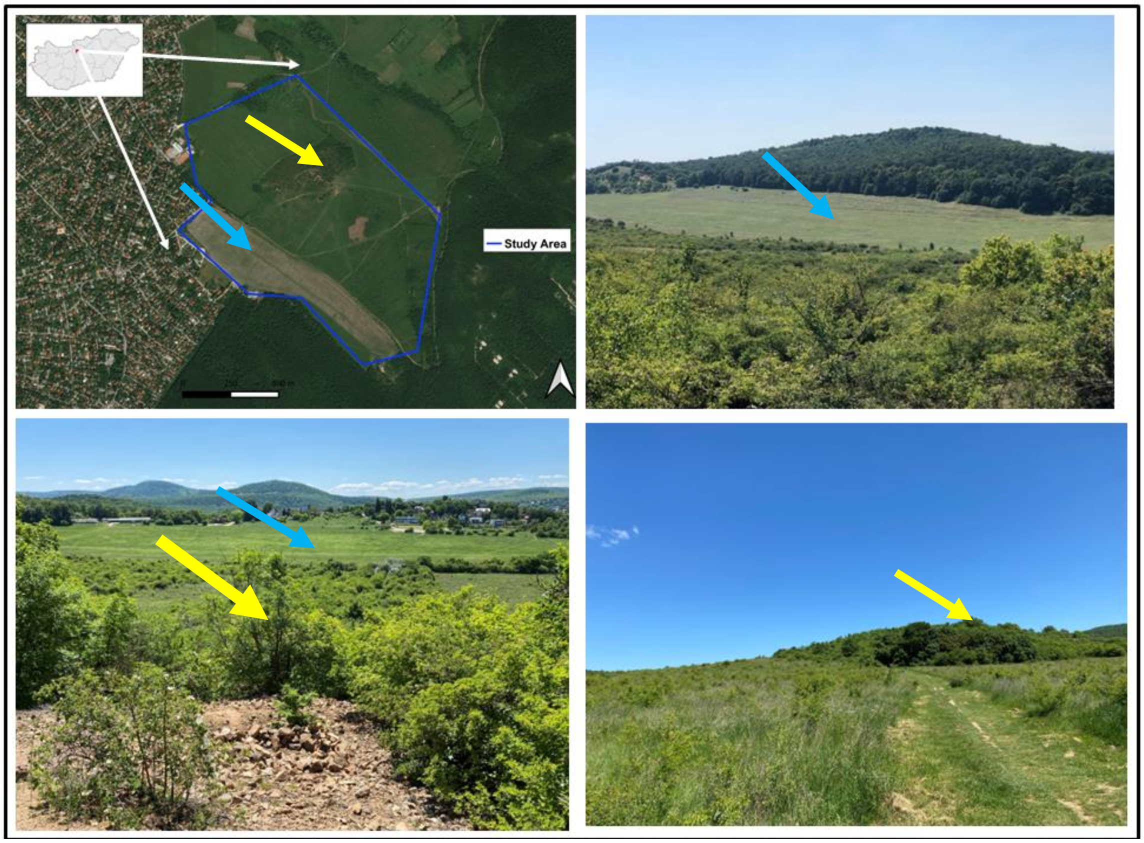


Figure 2: An aerial image showing the perimeter of a 125ha study area (top left) and images showing the physical attributes of the area. The blue arrows indicate the open grassy airfield as a type of patch in the area, while the yellow arrows show the rocky outcrop mount.

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.

3.2.2. Data collection

3.2.2.1 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, (Fig. 3) and analyzed using standard map grid cells of 20 x 20 m by QGIS (3.10v)).

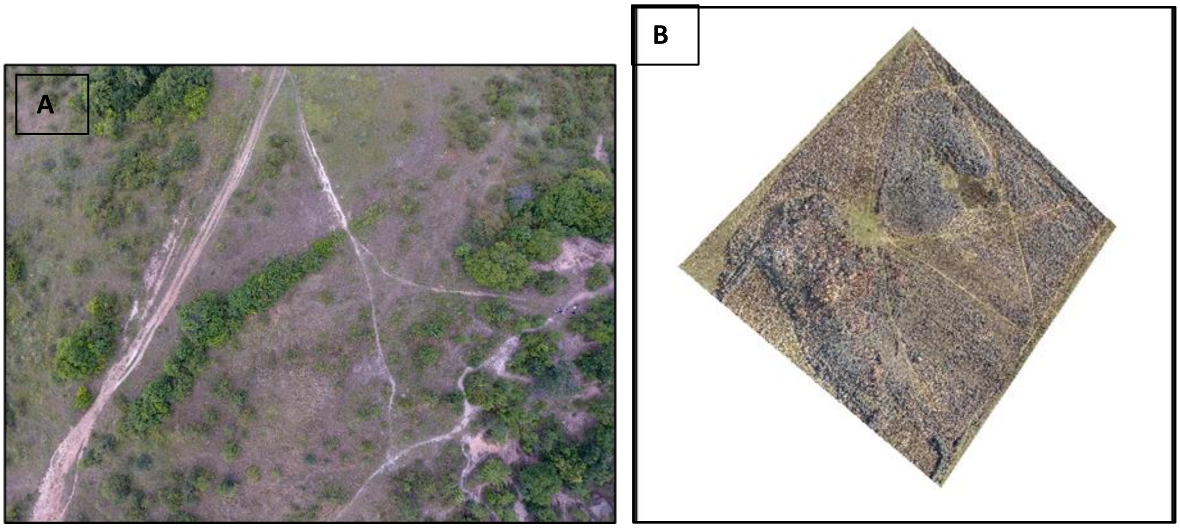


Figure 3: (A & B): A: A sample of an actual aerial image taken by the drone; and B: Ortho-mosaic image of 301 images stitched together using the DroneDeploy application.

3.2.3. 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.

3.2.3.1. 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 (see Fig. 4A). 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) (Fig. 4A). 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%.

3.2.3.2. Ungulate browsing impact.

3.2.3.2.1. 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) (Fig. 4A) 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 (Fig. 4B) 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).

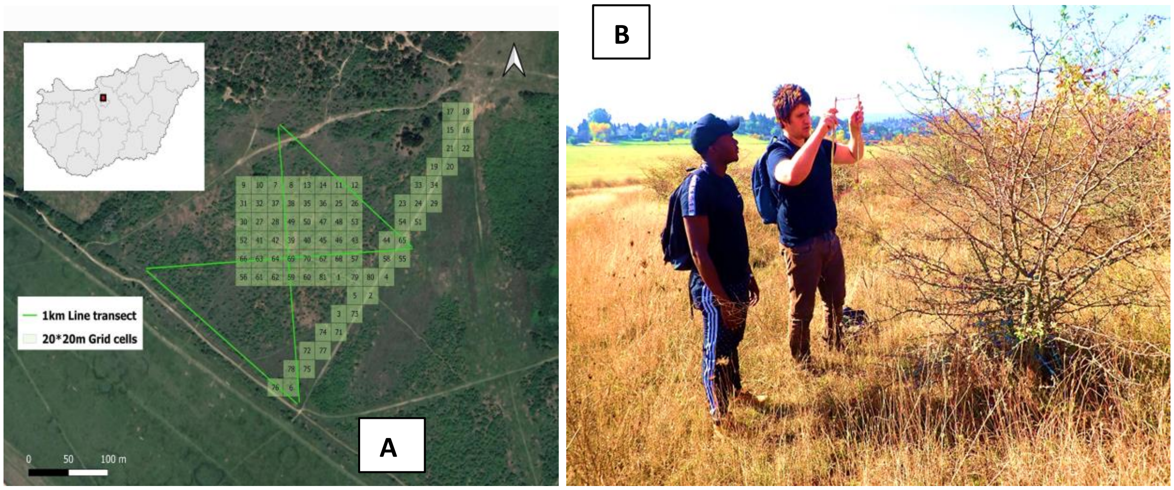


Figure 4: (A) design of transect line (green) in the study area for ungulate browsing data collection interacting with the area surveyed for shrub cover (B) Counting available and browsed shoots at different heights as food for ungulates.

3.2.3.2.2. 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 (Fig. 5).

Figure 5: Damage caused by ungulates on saplings 5(a); types of browsing (control), 5(b) & 5(c) images captured during field data collection on differently affected individuals (C-top browsed and O -laterally browsed).

3.2.4. 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 (Fig. 6a). 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 (Fig. 6b).

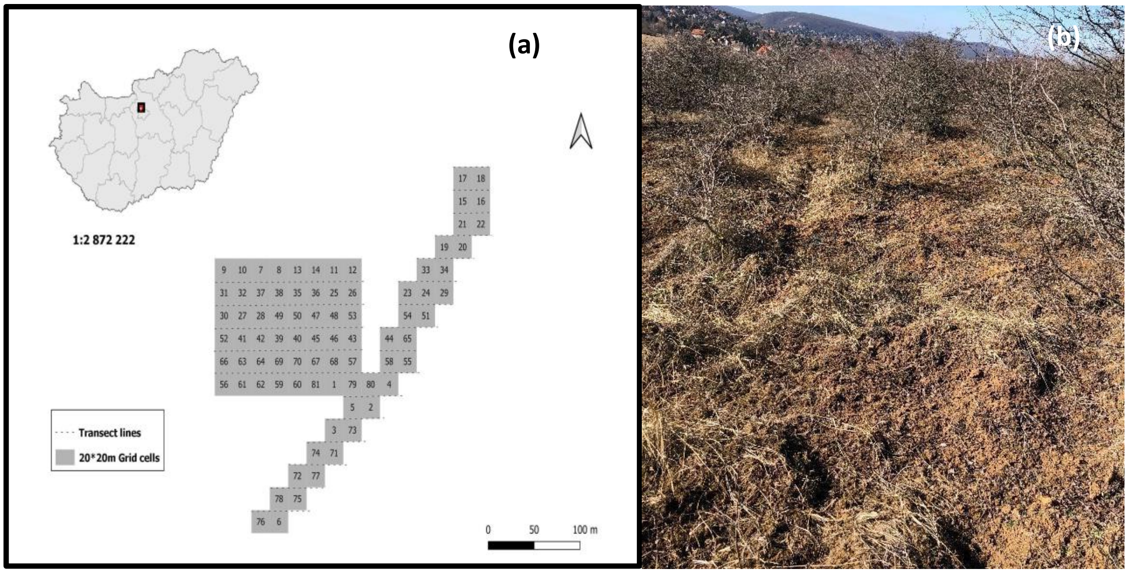


Figure 6: (a) A map showing the study location (top left), 20*20 grid cells, and the design of wild boar rooting sampling, including transects (right) and (b) wild boar rooted patch in the study area.

3.2.5. Space use of Caspian whipsnakes.

3.2.5.1. 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.

3.2.5.2. 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.

3.2.6. 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 (Fig. 7A-E). The number of pictures of snakes was counted per day and for 30-minute periods within days between sunrise and sunset.

Figure 7: Camera trap images next to burrows of Caspian Whipsnakes (A: great tit, *Parus major*, B and D: Caspian whipsnake, C: red fox, E: wood mouse, *Apodemus sp*.).

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.

3.2.7. 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 (Fig.

8) 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.

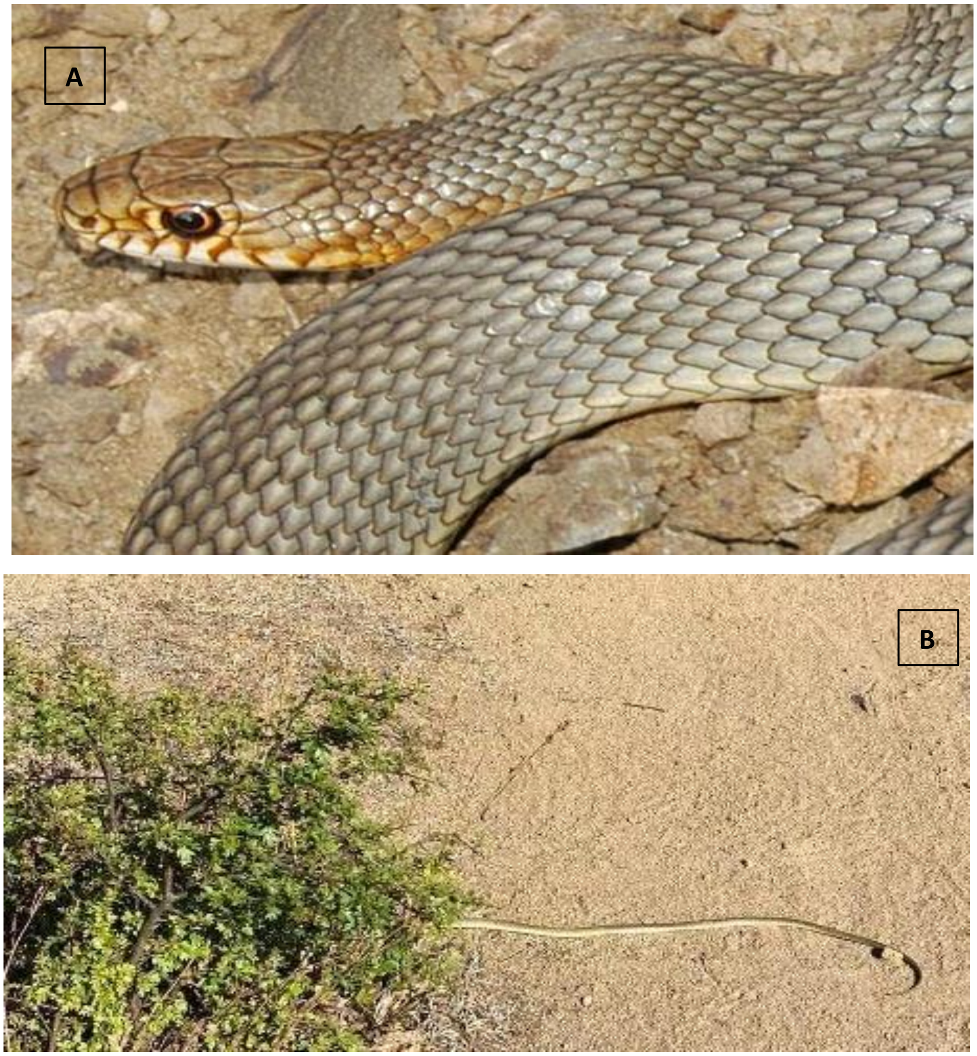


Figure 8: A: A real Caspian whipsnake captured by the camera in the field; B: dummy snake used in the field for the survey.

3.3. Data analysis.

The section focuses on the technical tools and techniques used to analyze data collected during the research period for both literature surveys and field-based research. The data was analyzed using both simple descriptive statistics and complex statistical tests applicable to scientific research. Our datasets were tested for normality using the Shapiro-Wilk test (Mishra et al. 2019).

3.3.1. 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).

3.3.2. Field based research

3.3.2.1. 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.

3.3.2.2. 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).

3.3.2.3. 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.

3.2.3.4. 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).

3.2.3.5. 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).

3.2.3.6. 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.

4. RESULTS

4.1.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**.**

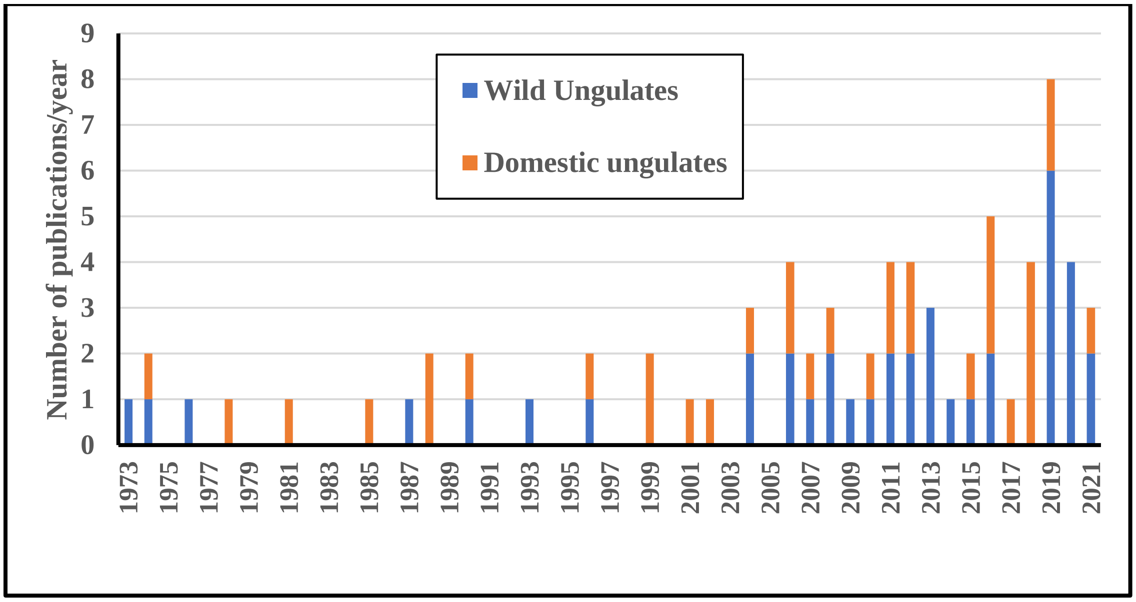


Figure 9: Number of publications per year (n = 73, including review papers) focusing on the impact of wild and domestic (livestock) ungulates on reptile species based on the selected publications of the search.

From our literature search results we can reiterate that studies on ungulate-reptile interactions have been gaining increasing attention by the scientific community in the last decade as there are more recent (2010 – 2021; n = 41) and fewer older papers (1973 – 2009; n = 32) (Fig. 9). More attention was given to livestock interaction with reptiles as opposed to wild ungulates in the 1973 – 2002 period (n = 12 and n = 7, respectively). Whereas wild ungulates and their interactions with reptiles have been researched more intensively in the past two decades (n = 30 and n = 20, respectively). We found that 64% (n = 44) of the papers published a descriptive study, 29% (n = 20) of them an experimental research and direct observational publications constituted 7% (n = 5).

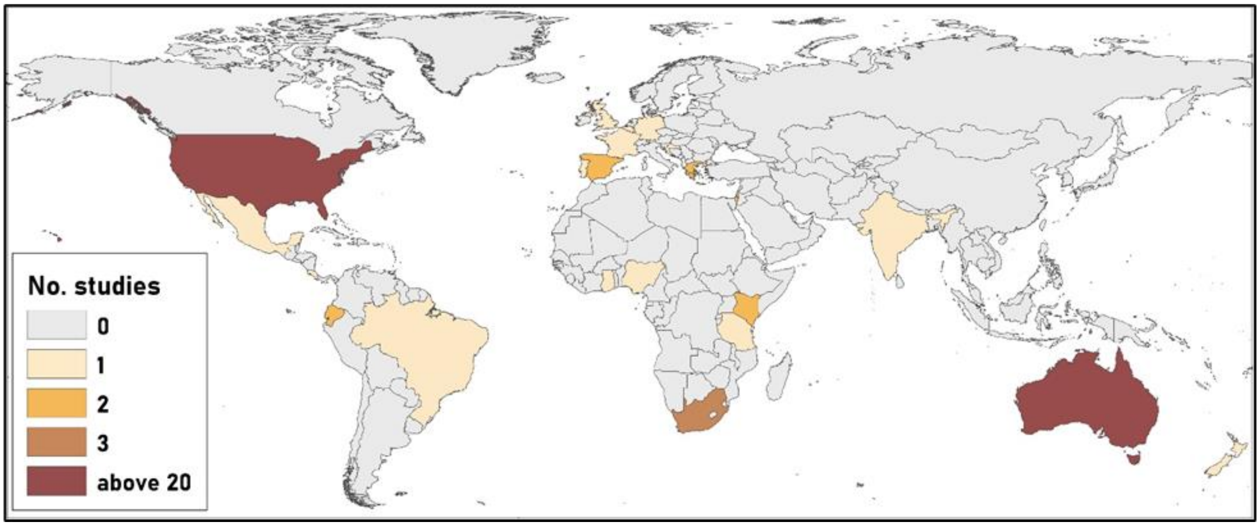


Figure 10: Number of publications per year (n = 73, including review papers) focusing on the impact of wild and domestic (livestock) ungulates on reptile species based on the selected publications of the search.

The geographical distribution of the studies shows that 42% (n = 29) of investigations were conducted in the Americas, 28% (n = 19) in Australia, and only 13% (n = 9) in Europe, 12% (n = 8) in Africa, 4% (n = 3) in Asia and 1% (n = 1) in Oceania (Fig. 10).

We found that 59% (n = 41) of the studies were conducted dominantly on terrestrial landscapes in mixed habitats (usually a mosaic of different macro- and microhabitat types; shrublands, grasslands, forest, woodlands, etc.). The remaining 41% (n = 28) took place in homogenous habitats; 21% on grasslands, 12% in forests, 6% on wetlands and 2% on shrubby areas. In some occasions studies were carried out near and linked to aquatic ecosystems; for example, in case of nest predation by wild boar on sea turtles.

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.

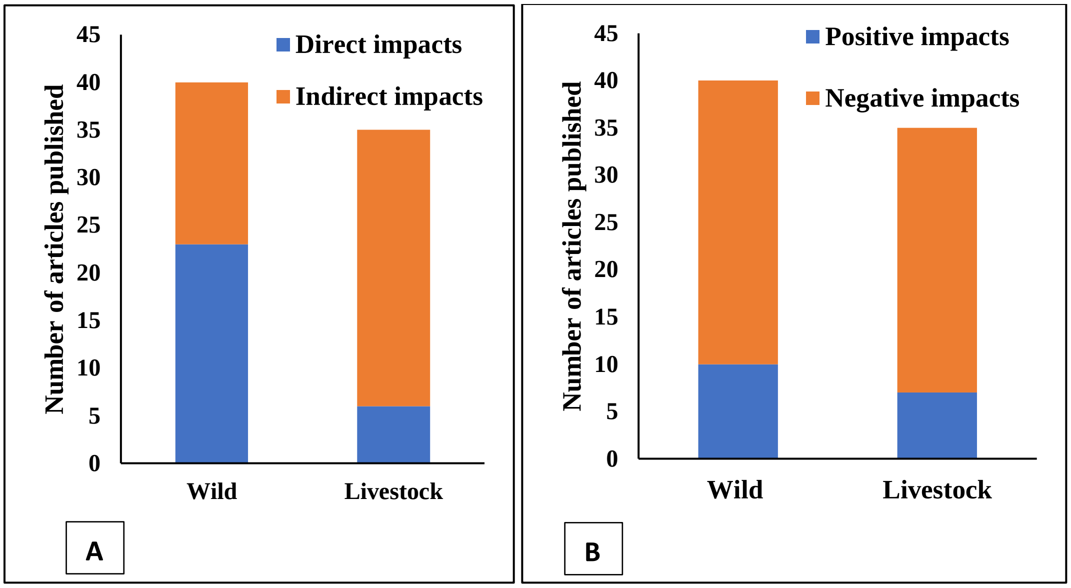


Figure 11: Different types of impacts (Fig. 11A: direct and indirect or Fig. 11B: positive and negative, respectively) on reptiles by wild and domestic ungulates based on the reported 75 interactions between 1973 and 2021.

Studies on impacts were balanced between wild ungulates and livestock in terms of their interactions with reptiles, showing a proportion of 53% and 47% (n = 40 and n=35, respectively (Fig. 11). We found that 61% of the interactions (n = 46) showed examples on indirect ungulate impacts and 39% of them (n = 29) were direct effects. Livestock caused indirect impacts on reptiles more frequently than wild ones (63%; n = 29 vs. 37%; n = 17), and the reverse was found for the direct impacts (Fig. 11A). The indirect impacts mostly included overgrazing and/or over browsing by livestock (i.e., removal of understory) whereas the dominant direct impact was found to be the predation by wild ungulates. For both ungulate species groups negative effects on reptiles were much more common (livestock 48%; n = 28 vs. wild ungulates 52%; n = 30) (Fig. 11B).

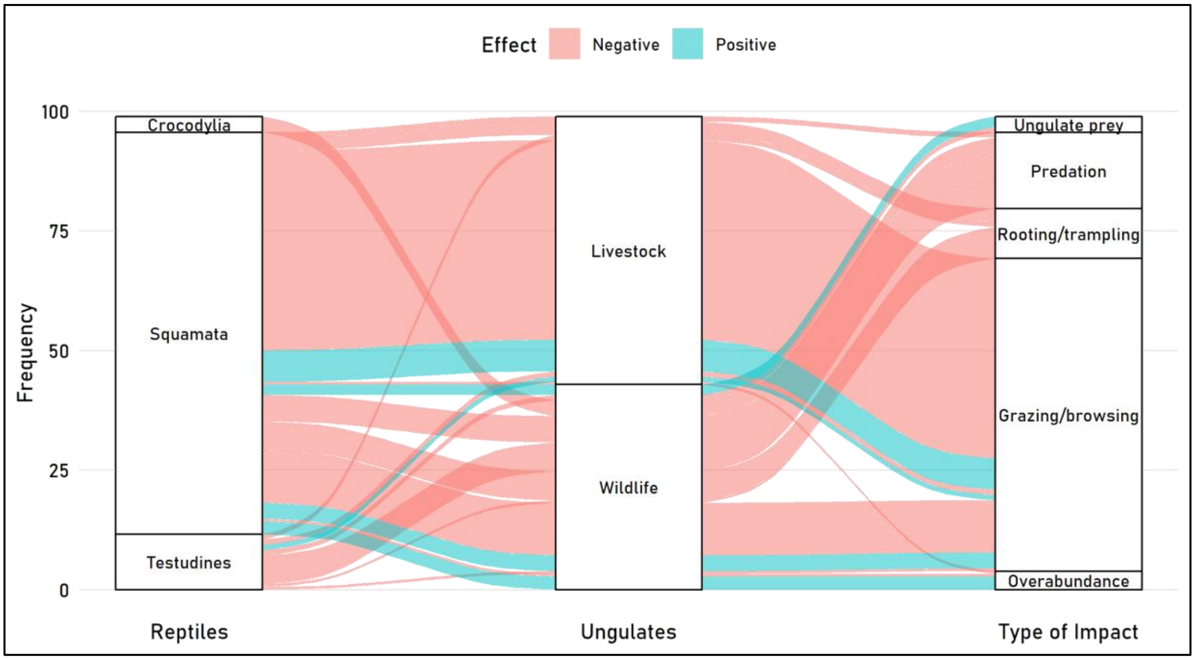


Figure 12: The distribution patterns (frequencies) of publications showing the different types of impacts / interactions of ungulates (wild ones and livestock separately) on / with different orders of reptiles.

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. 12, Appendix 2). 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 (Fig. 12, Appendix 2).

Squamates (i.e., lizards and snakes) were the most negatively affected reptiles by ungulates, variedly impacted by both, wild ungulates and livestock (Fig. 12). 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

4.2.Field – based research

4.2.1. Shrub density and distribution

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.

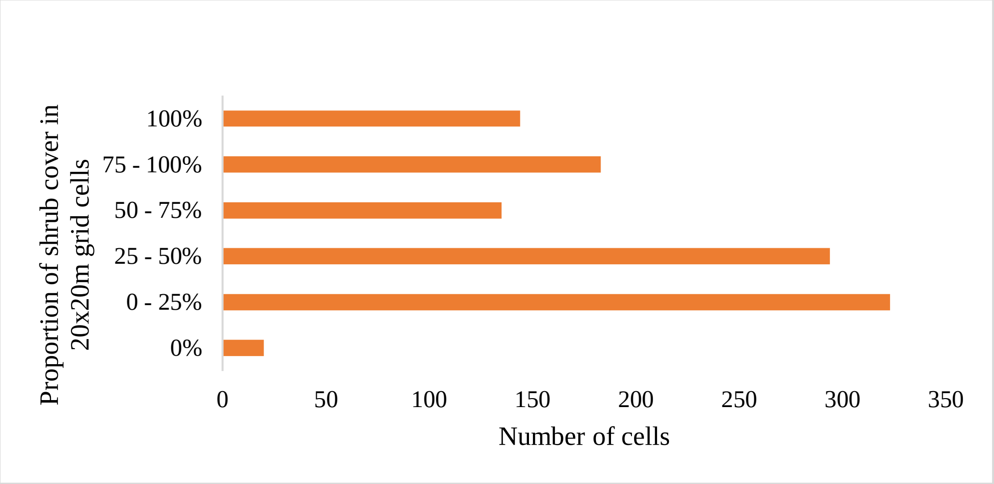


Figure 13: Estimated density of shrubs measured in cells.

The total number of 20*20m grid cells covering the area were 1099 (Fig. 13). Cells with 0 – 25% estimated shrub cover were found to be most dominating; n = 323. The cells with no shrub cover were least represented at 1.8% (n = 20) – open grassy airfield was not included in the grid. All the shrub cover categories were highly represented, this confirm the important finding that the area is indeed a heterogenous habitat consisting of different patches.

4.2.2. Survey on shoot availability for ungulates and browsing on woody species

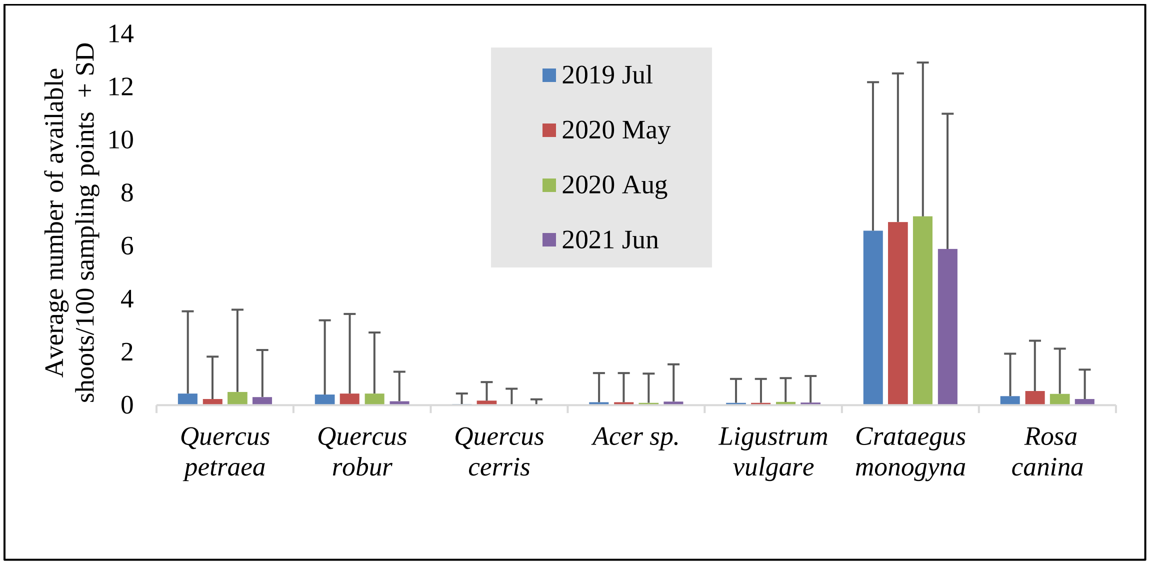


Figure 14: Average number of available shoots (food supply) in the study area during summer seasons on 100 sampling points along a 1km transect between 2019 and 2021.

The results of Friedman ANOVA revealed a statistically significant difference among the four treatment groups: ($X^2(3) = 36.74$, $p < 0.0001$). *Crataegus monogyna* was found to be the most available food supply (~70%) for ungulates in the study area throughout the years (Fig. 14).

Kruskal-Wallis test revealed a significant difference between the frequency of consumption of different available plant species throughout the seasons ($H = 7.88$, $df = 6$, $p = 0.032$). A pairwise comparison (Dwass-Steel-Critchlow-Flinger) showed that there were significant differences in the frequency of browsing between *Crataegus monogyna* and *Quercus petraea* and *Quercus robur*, *Quercus cerris* and *Acer sp. and Ligustrum vulgare (*P<0.05) in all the sampling seasons.

Between the seven available plants species in the sampling area, *Crataegus monogyna* was the most frequently browsed followed by *Rosa canina*, the least consumed species was *Ligustrum vulgare;* moreover, based on the Jacobs' selectivity index only *Crataegus monogyna* was preferred (Fig. 15).

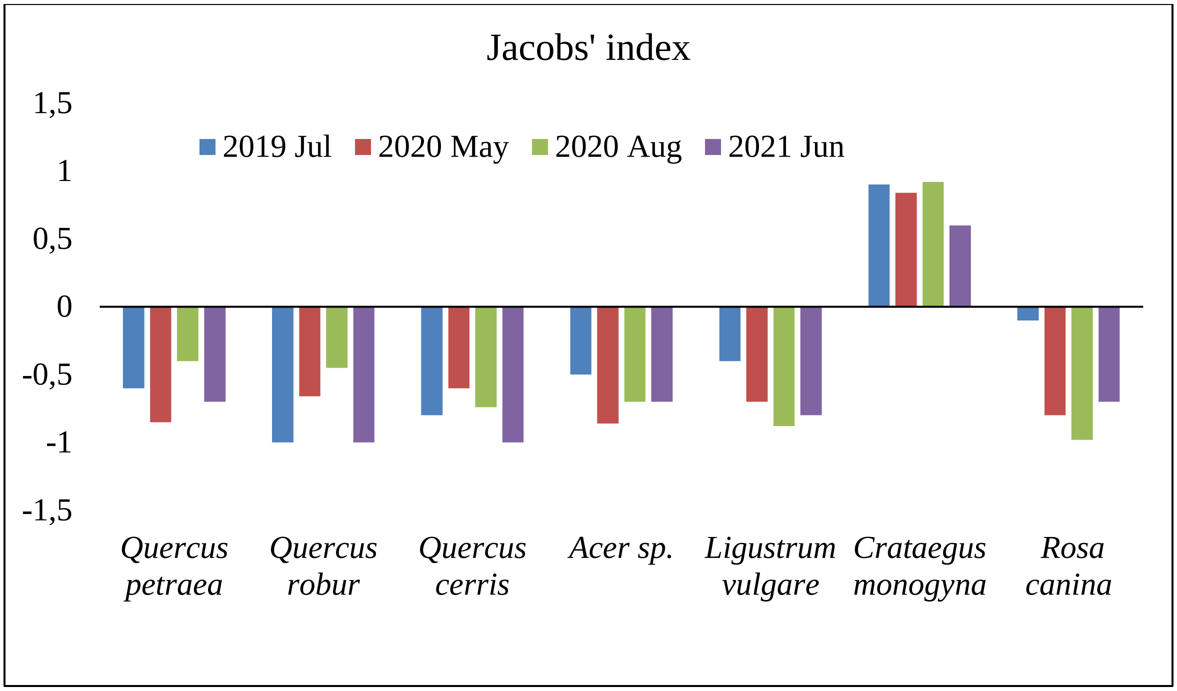


Figure 15: Selection (preferred or avoided) of plant species by ungulates in the study area.

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*.

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

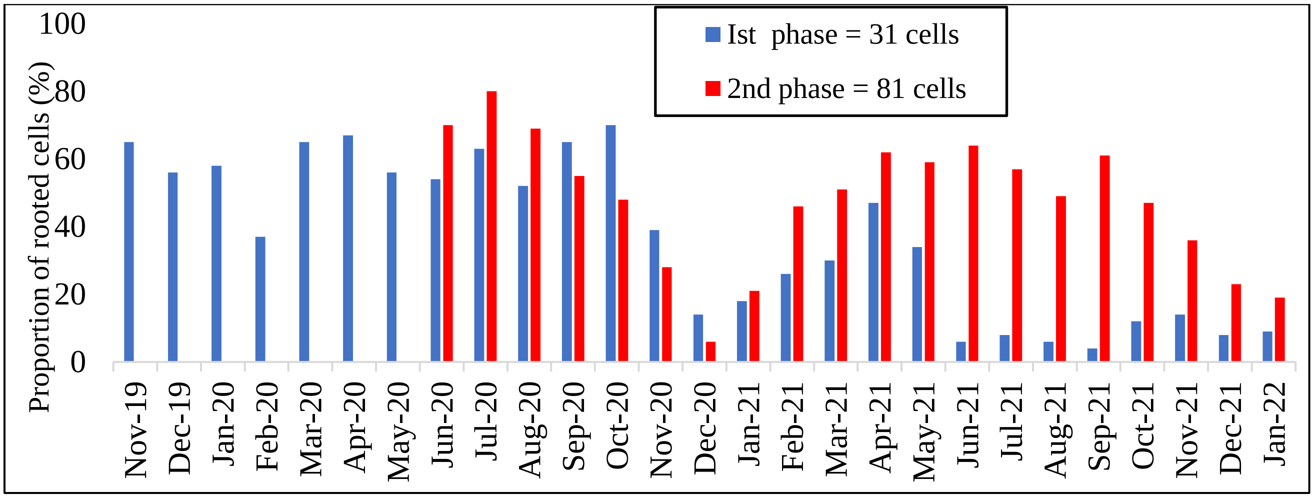


Figure 16: Wild boar rooting disturbance between November 2019 and January 2022.

Our results show that between November 2019 and January 2022 the average proportion of rooted cells in the study area was 41% (Fig. 16). The proportion of rooted cells has increased in spring and summer and showed lower values between November and February.

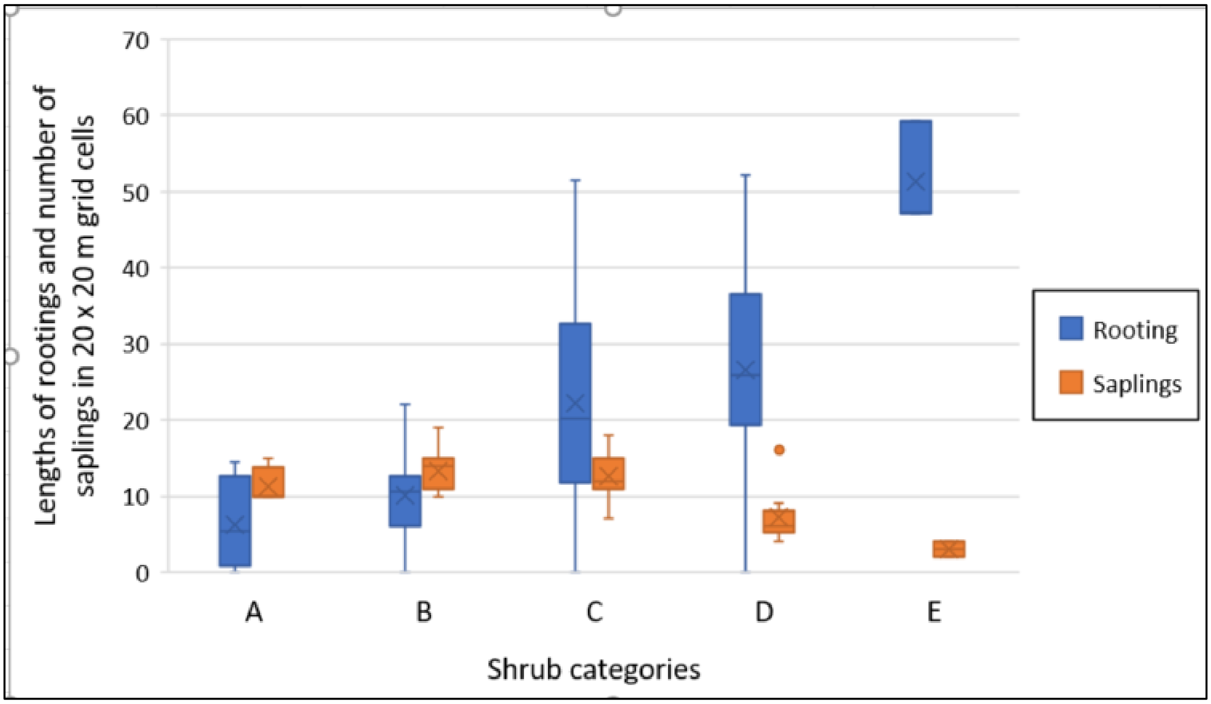


Figure 17: The intensity of rooting activities and average number saplings and their occurrence in cells with different shrub densities: (A: 0%, B: 1 – 25%, C: 26 – 50%, D: 51 – 75% and E: 76 – 100%). Box lines showing medians, upper and lower quartiles, whiskers providing the minimum and maximum values, circles being the outlier values, X-s giving the means.

There was a significant difference in the lengths of wild boar rooting occurring in cells with different categories of shrub density (Kruskal-Wallis test - $X^2 = 35.6$; $df = 4$; $p < 0.001$) (Fig. 17). 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 (Fig. 17). 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).

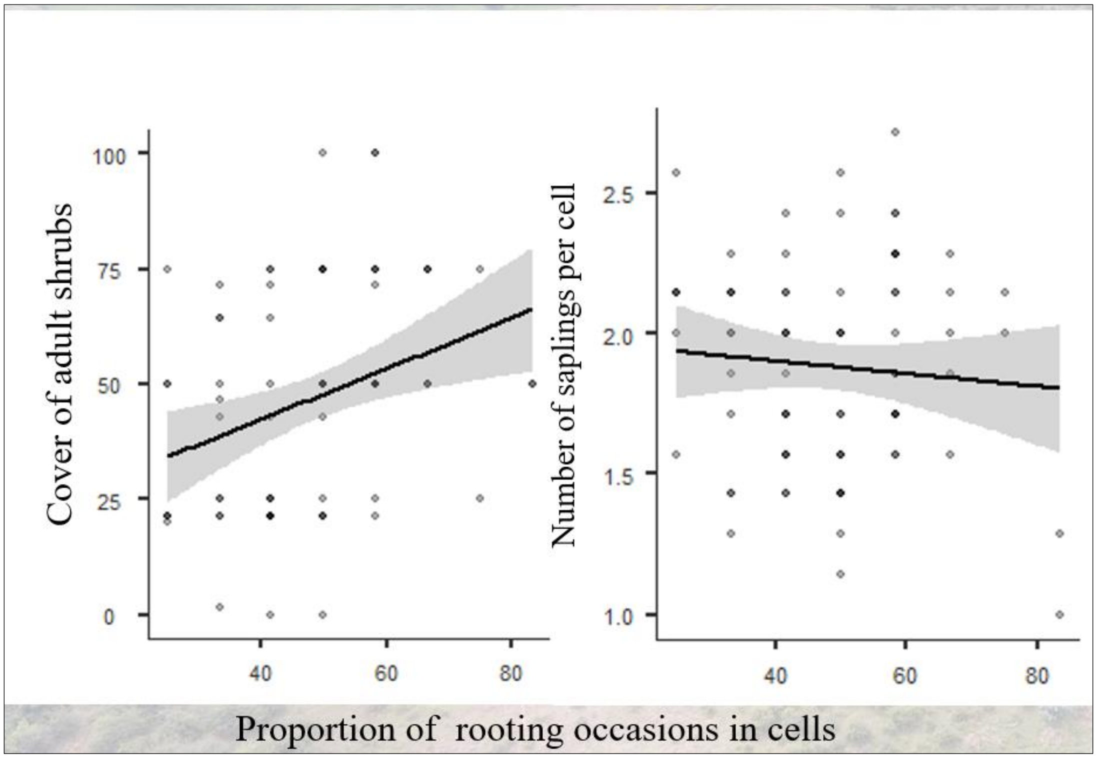


Figure 18: Correlation between rooting activity (proportion of occasions when rooting was found in a cell) and shrub density and saplings in the cells.

There was no significant correlation between the proportion of occasions when cells were rooted and sapling density in the cells (Pearson correlation: r= -0,084 p=0,461), but there was some positive correlation with shrub density in cells (r=0,388, p<0.001) (Fig. 18).

Furthermore, we found a significant difference in the shrub density between less rooted (<50%) and more rooted (>50%) cells (Kruskal-Wallis test: $X^2 = 34.4$; *df* = 4; *p* = 0,001).

4.2.3. 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 of first localisation	Date of last localisation	Number of localisation points				
				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 19).

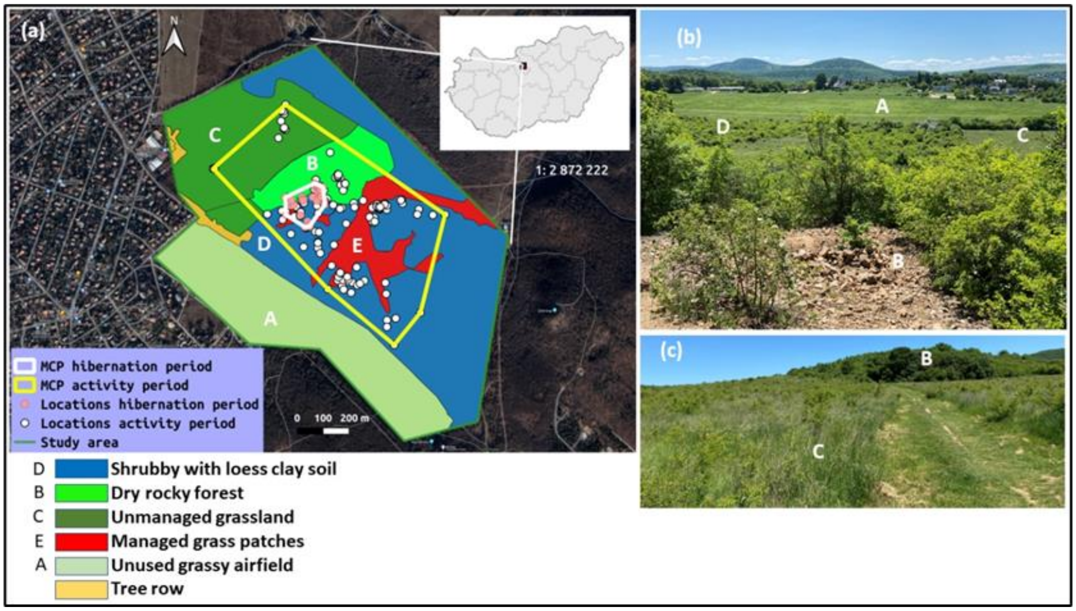


Figure 19: (a); Overall distribution of all localization points during activity period (n=226) and hibernation period (n=83) of five Caspian whipsnakes distributed in various habitat patches estimated by Minimum Convex Polygon (MCP) method: (b) and (c); images from the study area depicting different habitat patches. Capital letters on (a) correspond to those on (b & c) showing some of the habitat types.

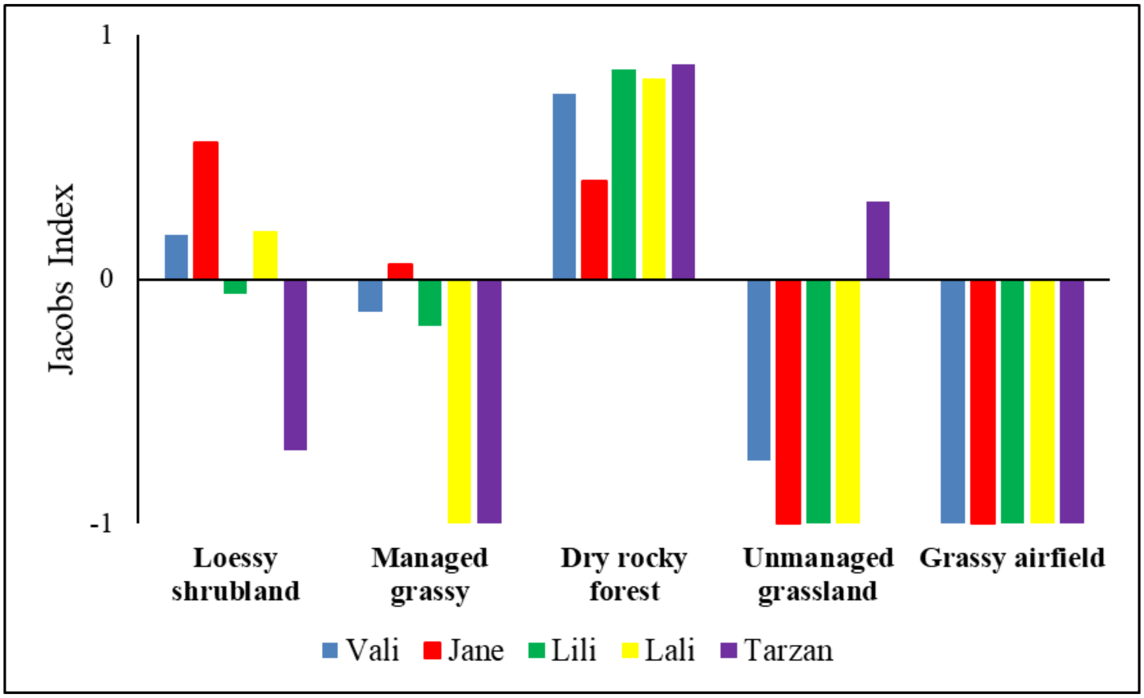


Figure 20: Jacobs' index values showing microhabitat preferences of Caspian whipsnake individuals in the study area.

Combining the localization points into one dataset, we found that Caspian whipsnakes prioritized the dry rocky forested patch with a high density of hibernacula and dens and the neighboring shrubland areas (Jacobs' index: D=0.78 and 0.10, respectively) but were much less detected in managed grassy patches and the unmanaged grassland (D=-0.40 and -0.38, respectively). The nearby grassy airfield was avoided (D=-1). Considering individual preferences (Fig. 20) snakes showed similar patterns, except that Tarzan was never localized in the shrubland but preferred the unmanaged grassland, meanwhile Jane was the only snake with a positive preference value in case of managed grassy patches.

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. 21).

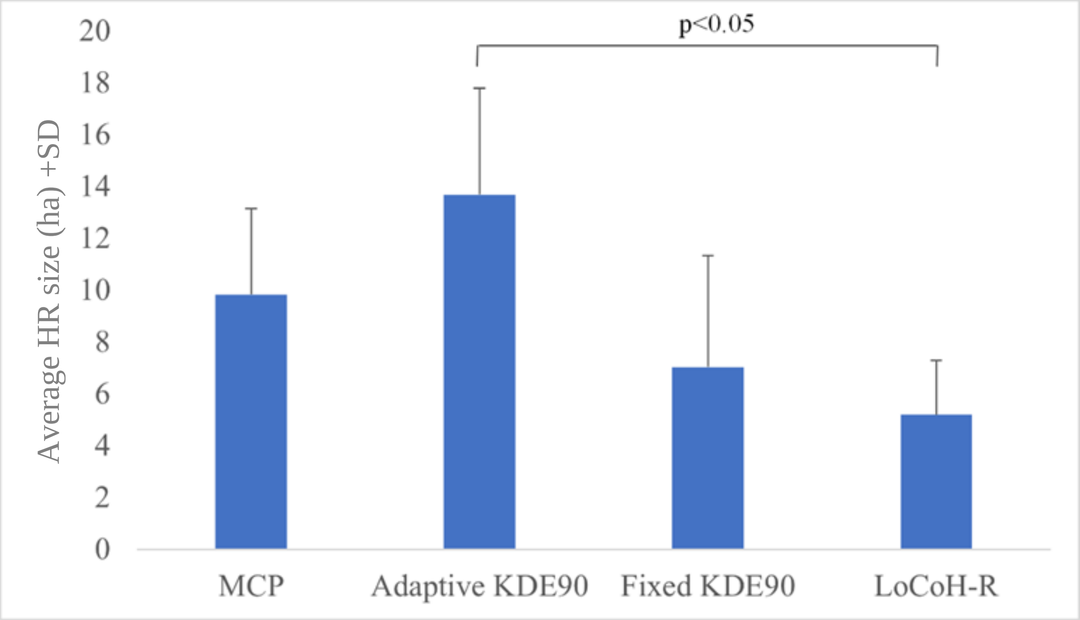


Figure 21: Average home range (HR) sizes calculated using the entire tracking dataset of all the years of tagged Caspian whipsnakes in the study area estimated by four different methods. There was a significant difference between adaptive KDE90 and LoCoH-R (p < 0.05).

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 (Fig. 22). 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.

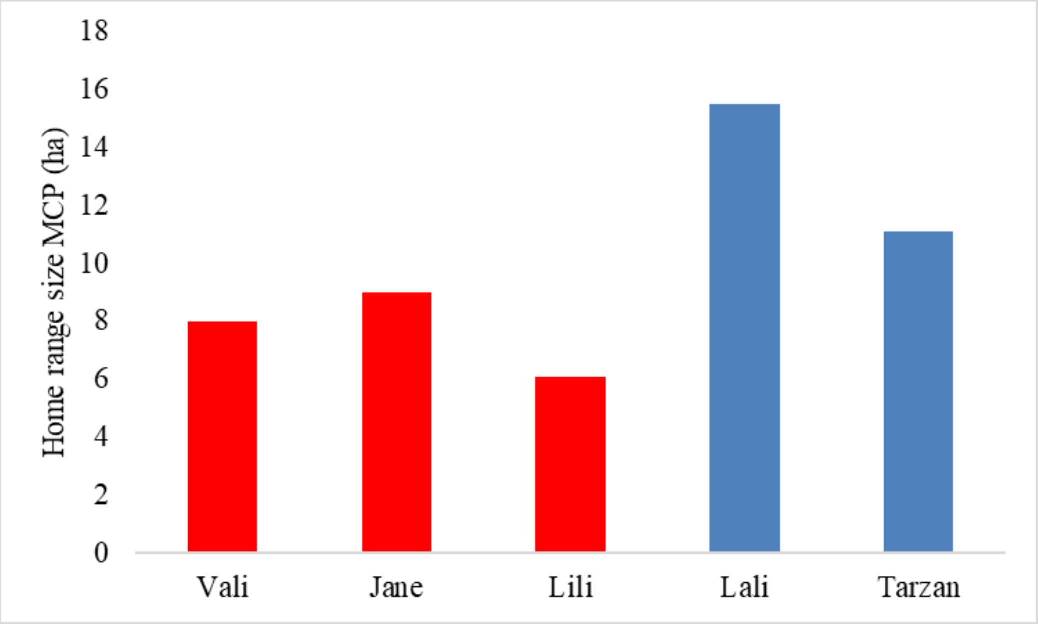


Figure 22: Individual home ranges sizes of Caspian whipsnakes calculated by MCP during the activity period. (Red bars: females; blue bars: males).

In most cases the overlaps of individual home ranges were relatively small (<10%) during the activity period, however, for some female-male pairs the overlap reached as high as 23, 40 and 60% in three pairings (Fig. 23). When the overlaps were expressed as the percentage of the home range of each pair, the overlaps averaged 24% in male and 43% in females in female-male pairs.

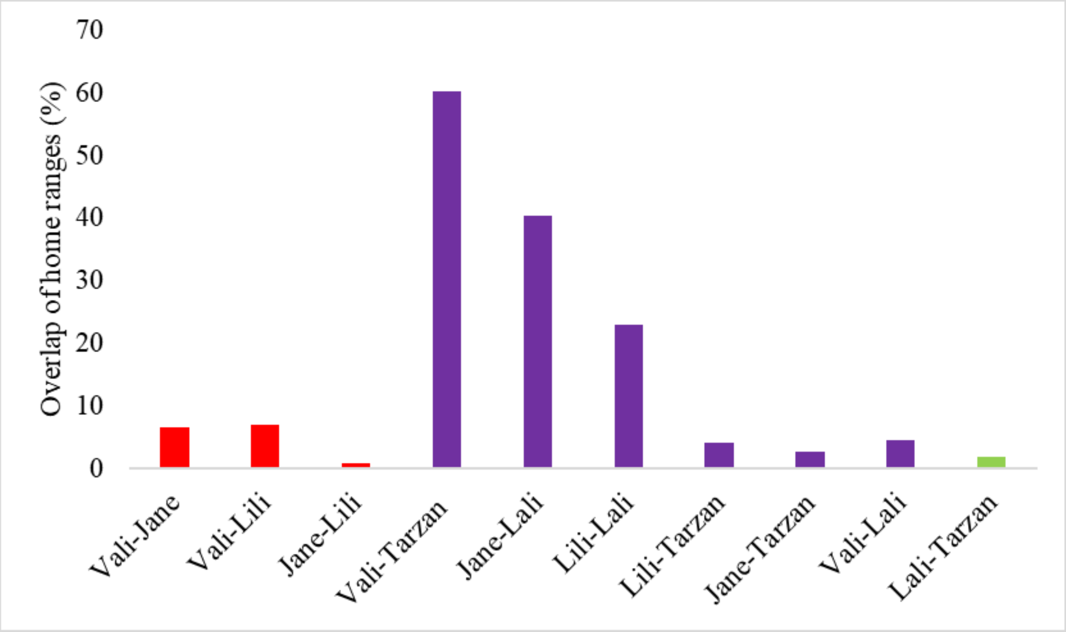


Figure 23: Overlap of the individual home ranges of Caspian whipsnakes as a percentage of the total area covered by the home ranges of the pairs (%) calculated by MCP during the activity period. (Red: female-female overlap, purple: female-male overlap and green: male-male overlap).

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 (Fig. 24). The maximum absolute value of the daily displacement during the activity period was found to be 226 m by Vali.

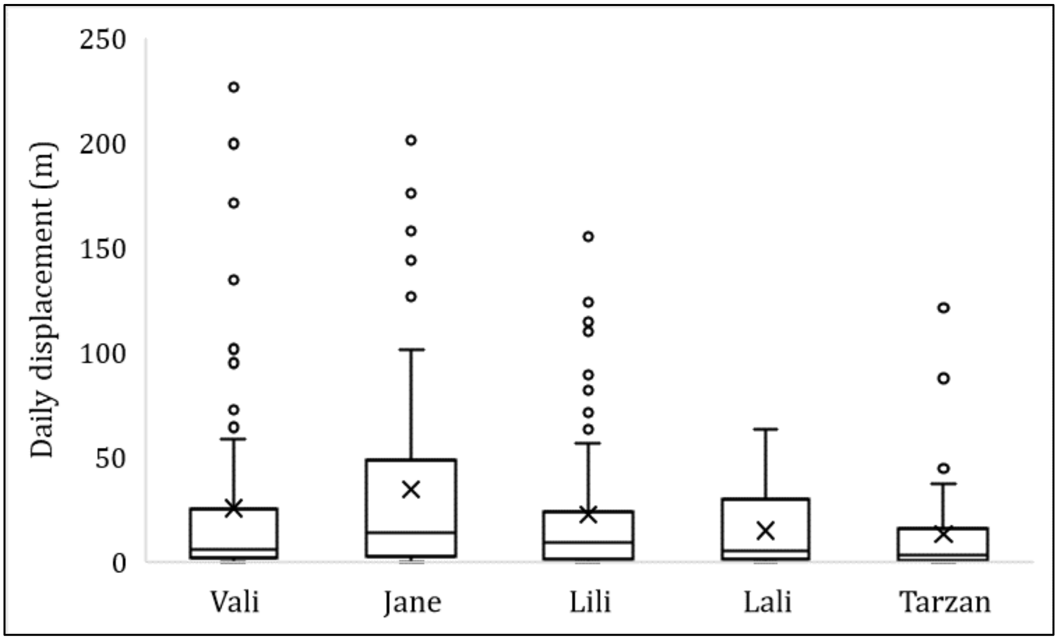


Figure 24: Daily displacements of five Caspian whipsnakes during the activity period (box lines showing medians, upper and lower quartiles, whiskers providing the minimum and maximum values, circles being the outlier values, X-s giving the means). No significant difference was found among individuals.

However, we found a significant temporal variation in the daily displacements of snakes throughout the year (Friedman ANOVA: $X^2 = 27$; $df = 9$; $p = 0.001$). Durbin-Conover pairwise comparisons showed that the daily displacements of the snakes in March and December were significantly lower than those of the other months. In August the movements were longer than in June or July or in the autumn months (Fig. 25). Except for a peak in August, no predictable temporal pattern of daily displacement distance was identified for either sex (Fig. 25B, C).

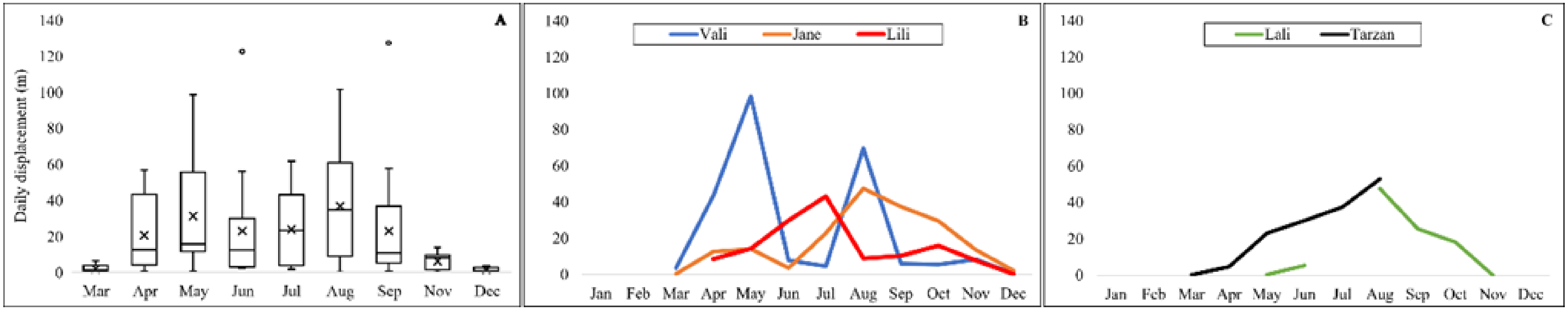


Figure 25: Daily displacement of five Caspian whipsnakes throughout the years. We found a significant temporal difference in daily displacement between the months, the value in August was significantly higher meanwhile in March and December the daily displacement were significantly lower than in other months ($p<0.05$). B and C: Average daily displacement in female and male Caspian whipsnakes (*D. caspius*), respectively, throughout the years. (In January and February, there was insufficient data for analysis)

4.2.2.1. 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.

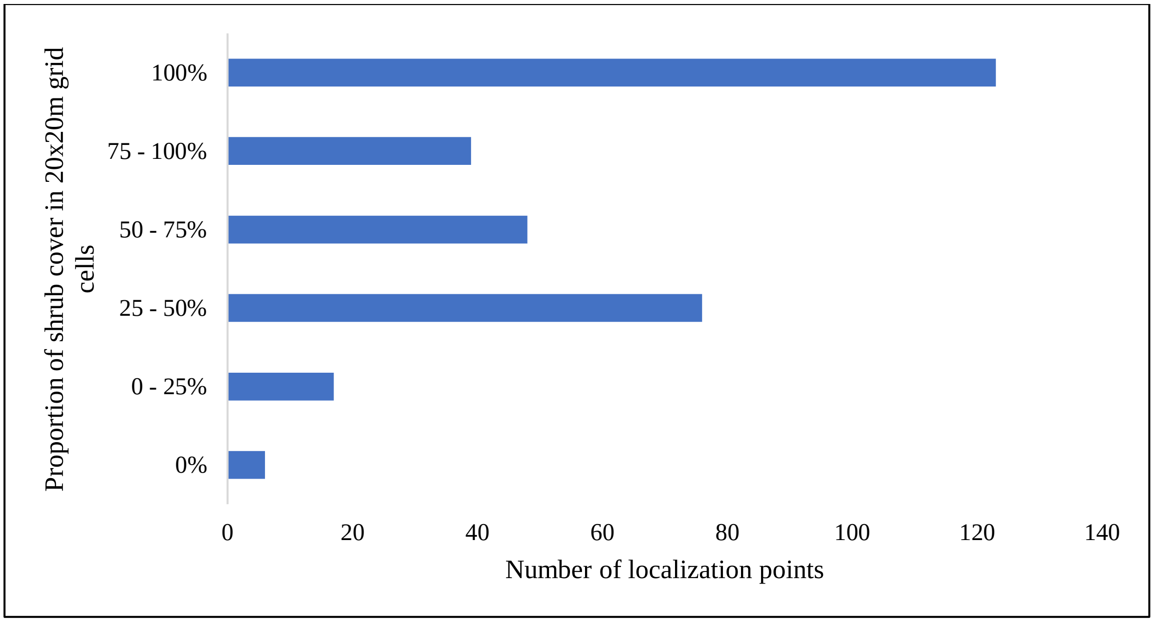


Figure 26: Number of Caspian whipsnake localization points found in cells with different shrub densities.

The highest number of snake location points were found in highly dense patches, 75 – 100% and 100%, respectively. 40% (n = 123) of the location points were found in cells with 100% shrub cover and 13% (n = 39) were found in cells with 75 – 100% shrub cover. Most importantly 25% (n = 76) and 5% (n = 17) of the snakes were recorded in cells with moderate shrub cover. We detected the least number of snakes (2%; n = 6) in totally open cells with no shrub cover (Fig. 26).

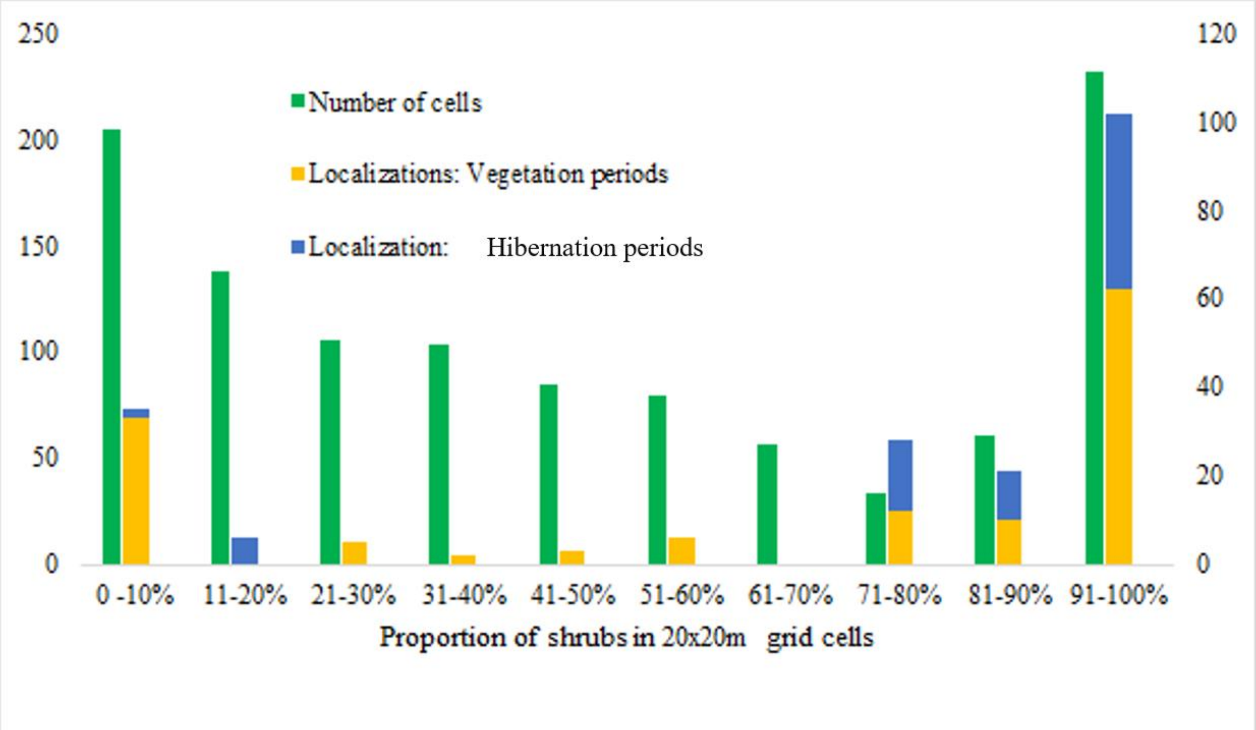


Figure 27: Caspian whipsnake shrub cover utilization during vegetation and hibernation periods.

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%) (Fig. 27).

4.2.4. Caspian whipsnake activity and possible threats in the peri-urban environment

The two cameras together captured 213 304 images on 14 occasions (3-4 days each occasion; meaning an average of 7618 images from each camera per occasion). No snakes were found in the images of Camera 1, however, Camera 2 captured 800 snake images (0.75% of pictures taken). Apart from Caspian whipsnakes, other wildlife species which appeared in the images were birds, most importantly the common black bird (T*urdus merula*) and great tits (*Parus major*) during the days and slugs only at night (between 21:00-03:00) on both cameras. We also captured the red fox (*Vulpes vulpes*) on one occasion. However, there was no detection of any ungulate species near to the investigated burrows of Caspian whipsnake.

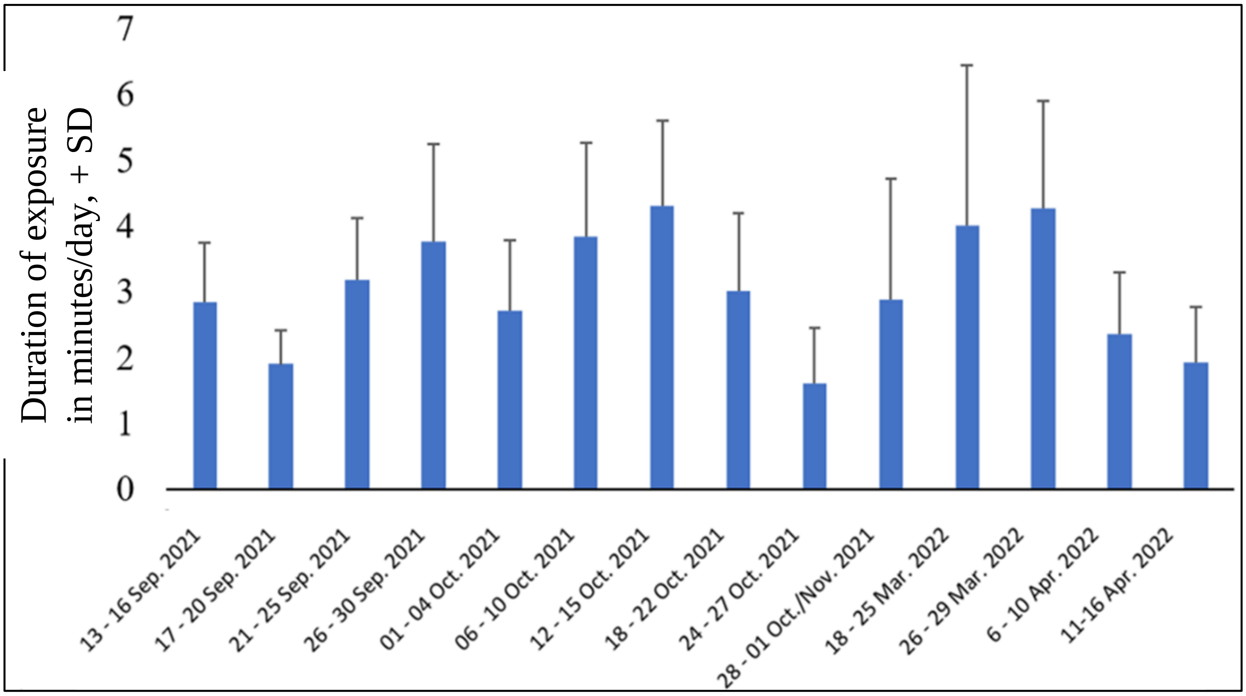


Figure 28: Time spent by Caspian whipsnake out of the burrow and surrounding vicinity of the camera trap.

Upon emergence on the surface, the snake spent approximately 2–4 minutes around the burrow (Fig. 28). The snake spent the least time aboveground in late October (mean = 1.61 min/day). The maximum spent time around the burrow was found to be 8 min/day. Only daytime observations of the snakes were registered.

4.2.4.1. 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.

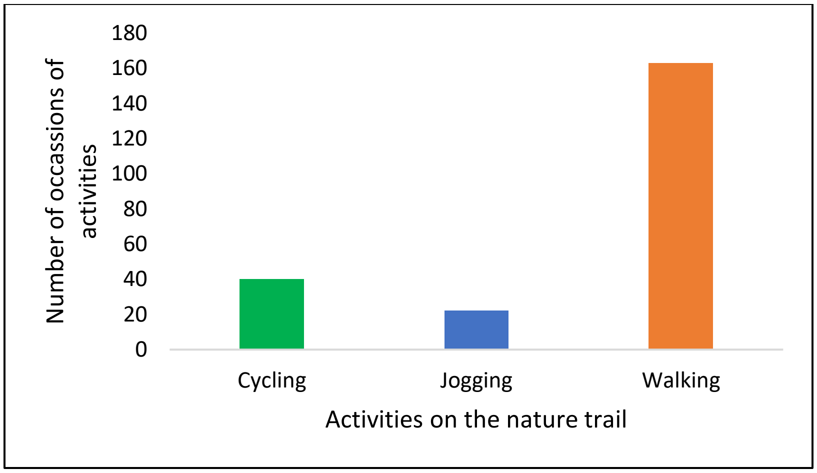
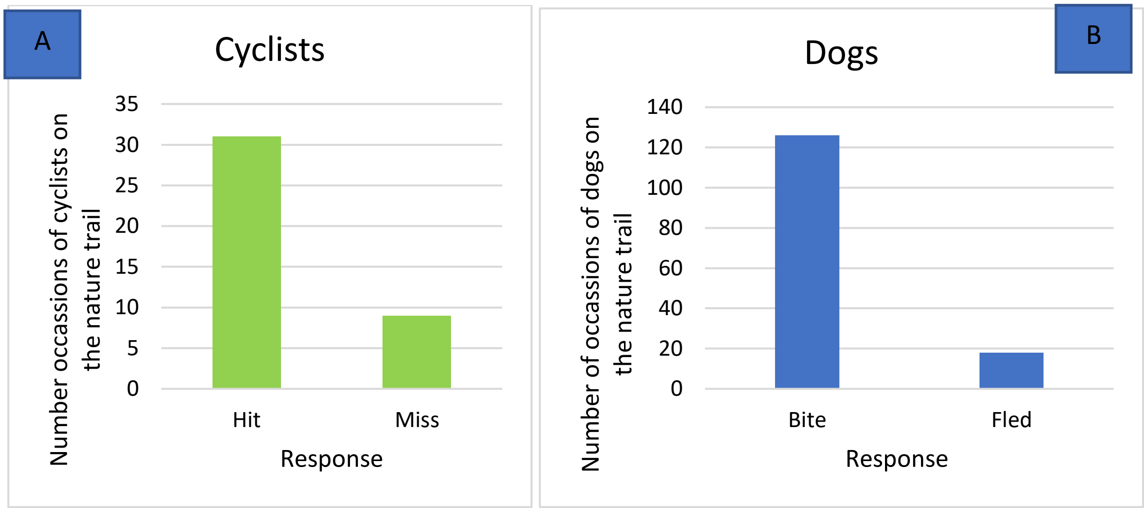


Figure 29: The total number of occasions of activities on the hiking/nature trail over 28 sampling days.

There were more walking people on the nature trail than cyclists and jogging individuals (Fig. 29). On 144 occasions walkers on the trail were accompanied by dogs, and all dogs were unleashed and freely moving ahead of the handler/owner.



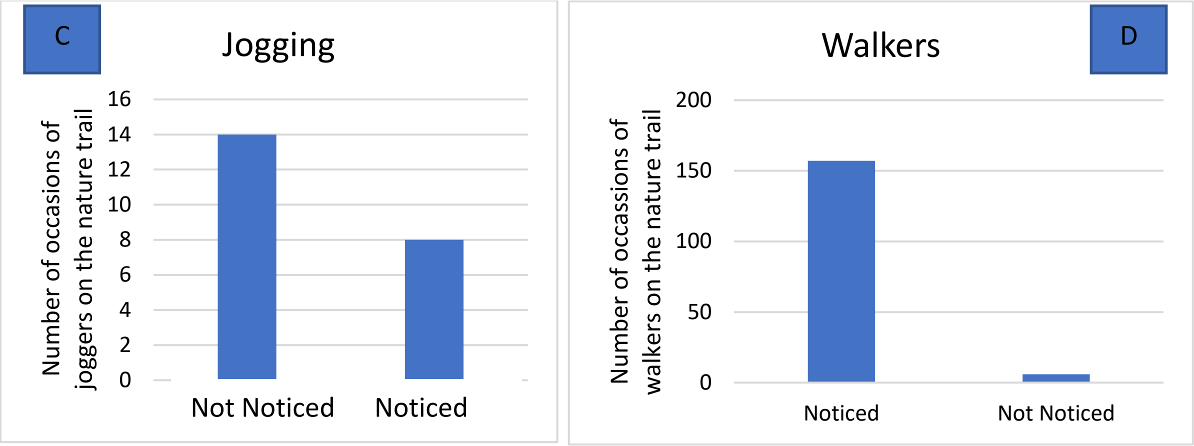


Figure 30: A, B, C and D: Number of occasions when cyclists, dogs, joggers and walkers were surveyed on the nature trail, respectively. The proportions of occasions are demonstrated when the dummy snake was detected, contacted or not contacted.

We recorded 40 occasions of cycling activities, 22 jogging activities, and 163 walking occasions (Fig. 30). 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.

Figure 31: A dog attempting to kill a dummy snake during the survey (photo by Teffo T.R.)

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 (Fig. 31).

5. DISCUSSION

5.2. Literature survey: ungulates interactions with reptiles

The sporadic geographical distribution of studies suggests that ungulate-reptile interactions receive significantly different levels of attention globally from the scientific community. Relative to the reptile diversity of the continents, an increasing number of studies is expected from Asia, Africa or South-America. Previous research reported distinct impacts and interactions between ungulates and reptile communities on different continents. For example, in Australia, where all ungulates are non-native and the ecosystems are more sensitive to their effects, the studies revealed significant impacts in the form of grazing effects by livestock (e.g., cattle; *Bos taurus*) (Fischer et al., 2004; Friend and Cellier, 1990; Val et al., 2019) or predation by wild ungulates (i.e., wild boar on marine turtles) (Nordberg et al., 2019), meanwhile in Asia the predation of reptiles on ungulates (Komodo dragon on Javan rusa, *Rusa timorensis*) (Ariefiandy et al., 2020) was a particular interspecific relationship. Although the largest part of the studies was a descriptive one providing mainly correlational information, the significant number of experimental studies (by manipulation of ungulate presence) also support the various ungulate effects on reptiles by more reliable methodologies of impact assessments.

We found that 59% of the studies took place in heterogenous habitat types (a mixture of shrublands, open grasslands, woodlands, wetlands, and riparian habitats). Mixed or mosaic areas are typical habitats for reptiles (Bateman and Merritt, 2020), and therefore studies are important in supporting habitat management and species conservation efforts.

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.

5.2. Field-based research

5.2.1. 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.

The advantage of using drones and other light unmanned planes is their ability to reduce human error, owing to their predefined automatic flight plans (Anthony et al., 1995). Field data accumulated from UAVs is readily georeferenced and make it possible to link information from different spatial and temporal scales (Jones et al., 2006; Martin et al., 2012) using automated software (DroneDeploy). The long process of acquiring permission associated with air-traffic control before the flight and the logistics form part of the disadvantages of using drones. Additionally, data captured by UAVs may be of high resolution and require high storage capacity and fast processing ability of the computer while working with the data (Linchant et al., 2015).

5.2.2. Shoot availability and browsing on woody species

The studied portion of the area was occupied by seven woody species which may potentially contribute to shrub encroachment. 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.

5.2.3. 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. From Figure 15 of the results, 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.

5.2.4. 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).

5.2.5. 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 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. However, 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.

5.2.6. 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.

Besides their well-known threats such as road traffic and habitat fragmentation, Caspian whipsnakes are becoming victims of anthropogenic activities either directly and indirectly, through direct killings, tourism and recreational activities, for example, Christopoulos and Zevgolis (2023) found a Caspian whipsnake entangled by a fishing net on the shore of an ocean in Greece.

6. 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 can mitigate 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 non-gravid 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 is 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.

7. 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.

8. SUMMARY

Several ungulate species are showing increasing population patterns within their geographical distribution ranges, leading to constant interactions with other animal species. Ungulate activities can have significant top-down effects on the structure of plant communities resulting in indirect impacts on the habitat of other animal species. Varying densities and activities of different ungulates may result in diverse impacts on other coexisting species groups, including large numbers of threatened species, such as reptiles. Our research explores ungulates impacts and their interactions with reptiles and their habitats, to achieve this we conducted our research using an integrated approach which include 1) broad literature survey which describes the effect of ungulates on reptiles in different continents, and 2) A technical field-based research to achieve the main objectives.

Firstly, for the broad literature survey we aimed to reveal the diversity of: (1) the geographical and environmental distribution of related investigations; (2) the ungulate and reptile species involved; and (3) the characteristics of interactions (direct or indirect, positive or negative) from 69 publications. Our results show that the most papers were reported from the Americas (42%) and Australia (28%). The proportions of studies were balanced for wild ungulates (53%) and livestock (47%). 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). Published livestock impacts were mainly indirect and mostly negatively linked to overgrazing. We conclude that it is important to manage and monitor the densities of ungulates to minimize their negative impacts on reptile species, especially in case of wild boar and grazing livestock, but also to maintain their moderate beneficial effects (e.g., as prey basis).

Secondly our technical field-based research is mainly focusing the impact of ungulates in an urban habitat of a strictly protected Caspian whipsnake (*Dolichophis caspius*). We surveyed an area of 3.2 ha in Vöröskővár in Budapest, where shrub encroachment is a threatening factor. Our investigation followed an integrated methodological approach where 1) We investigated changes in vegetation cover in the study area over time, using field observations and Unmanned Aerial Systems (UAS). To achieve this, we captured aerial images by Phantom 4.0 drone and converted the images into an ortho-mosaic using Dronedeploy, then digitized the shrubs from the ortho-mosaic and calculated the area covered by shrubs and shrub density in 20x20m grid cells 2) We monitored herbivore impact on shrub encroachment process through browsing (on woody species and saplings) and rooting activity by wild boar. To fulfil these objectives, we collected GPS data of rooted patches monthly in designated adjacent rows of 20x20m grid cells parallel to each other (n=81), and estimated by field observations the area covered by rooted surface and availability of woody vegetation in each cell. Parallelly, we evaluated the relationship between deer pressure and plant food supply, using a special wooden frame of 50x50x30cm while counting the number of available and browsed woody shoots along a 1km discontinuous transect 3) We further investigated preference of habitat patches by Caspian whipsnake in relation to their spatial movements in the study area. To achieve this objective, we investigated the spatial ecology of Caspian whipsnakes (*Dolicophis caspius*) in the area. We used radiotelemetry to track five adult snakes and analyzed their microhabitat preferences, home range sizes and daily movements. And 4) lastly, we investigated possible direct human and wild predator impacts on the Caspian whipsnake. To achieve these last objectives we used camera traps at the burrows of the snakes, additionally we investigated the human disturbance on the Caspian whipsnake in the area by placing a dummy (fake) 1.5m plastic snake resembling the Caspian whipsnake and noted the interactions and reactions to humans in the area.

Our investigation on shrub cover estimation in the area revealed that 51% of cells were covered with less than 45% shrubs (0 – 40%), implying availability of some open patches among shrubs. Resulting in a heterogenous habitat which is more suitable to snakes. Our result further revealed that there were less saplings in cells with more rooting and more saplings in cells with less rooting even though there was no significant difference in the number of saplings in different shrub density areas. We found that browsing pressure may have much less impact on the shrub encroachment process in the area. Jacobs' index showed that most of the species are avoided by deer and more than half of browsing was on the dominant species, namely on *Crataegus monogyna.*

With regards to the spatial ecology of the Caspian whipsnakes, our results show that the snakes intensively utilized areas covered with woody vegetation, with a high density of hibernacula. 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. During the activity period the individual home range sizes varied between 6.1 and 15.5 ha, estimated using the minimum convex polygon (MCP); however, for the entire datasets of the individuals, the adaptive kernel method gave the highest mean (13.8 ha), while the LoCoH-R yielded the smallest home ranges (5.19 ha). We found that the average daily displacement for the different individuals ranged between 12.6 and 36.6 m during their main activity season.

Using camera-traps we could not detect wild boar or other ungulates at the burrows of the Caspian whipsnake, only red fox was detected once. But when we investigating the interactions between human and Caspian whipsnake experiment 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 an over the snake and 23% (n = 9) missed the 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 have stopped for the dummy snake to observe. Additionally, we reveal that the most activity on the nature trail is walking. The dummy snakes were noticed 87% (n = 142) of the occasions. These 142 people stopped to observe the snake and was not afraid of it. However, they were in many cases not aware that it is a dummy snake. On 9% (n = 15) of the occasions the walkers fled when they so the snake, they were afraid. On occasions (n = 3) where people are walking in a group they hit or stepped on the snakes all the times. Dogs attacked the snake in the most cases.

Above all the existence of this isolated population of Caspian whipsnake may indicate and suggest that the peri-urban ecosystem is in a good health state. This implies, that the area has both a functioning food-web (from ungulates, birds, reptiles, invertebrates) and the necessary habitat complexity (a mosaic of patches). However, as our results prove that ungulates alone may not effectively halt the shrub encroachment process, management intervention should be considered in the area to monitor wild boar populations, as their rooting activity may play an important role in maintaining some open spaces in the habitat of the Caspian whipsnake. And lastly, management may consider physical trimming of shrubs to maintain the heterogeneity of the habitat.

9. ÖSSZEFOGLALÁS

Számos patás faj mutat állománynövekedést az elterjedési területén belül, mely különböző jellegű interakciókhoz vezet egyéb állatfajokkal. A patások viselkedésének jelentős felülről szabályozó hatása lehet a növényzet szerkezetére és összetételére, ami így az élőhely megváltoztatásával indirekt módon hat más állatokra is. A különböző patás fajok eltérő sűrűsége és tevékenysége különféle hatásokat eredményezhet más együttélő fajcsoportokra, beleértve nagyszámú veszélyeztetett fajt is, például hüllőket.

Kutatásunk a csülkös vadfajok hatását és kölcsönhatásait tárja fel a hüllőkre és élőhelyeikre. Ennek érdekében kutatásunkat integrált megközelítéssel végeztük, amely magában foglal 1) egy széleskörű szakirodalmi elemzést, amely leírja a patás fajok hüllőkre gyakorolt hatásait különböző kontinenseken, és 2) egy terepi vizsgálatokon alapú kutatást.

Először a széleskörű szakirodalmi áttekintéssel, 69 publikációból a következő szempontok sokféleségét kívántuk feltárni: (1) a kapcsolódó vizsgálatok földrajzi és környezeti megoszlása; (2) az érintett patás- és hüllőfajok; és (3) az interakcióik jellemzői (közvetlen vagy közvetett, pozitív vagy negatív kapcsolatok). Eredményeink szerint a legtöbb publikáció Amerikából (42%) és Ausztráliából (28%) származik. A vizsgálatok aránya kiegyensúlyozott volt a vadon élő patások (53%) és a legelő haszonállatok (47%) között. A vaddisznó (*Sus scrofa*) a legproblémásabb patás faj a hüllők szempontjából, míg a legerőteljesebb hatásokat elszenvedő hüllők a *Squamata* (azaz gyíkok és kígyók) voltak. A legelő haszonállatok leírt hatásai főként közvetettek voltak, és többnyire negatívak a túllegeltetés miatt. Arra a következtetésre jutottunk, hogy a patások állománysűrűségének kezelése és monitorozása fontos a hüllőfajokra gyakorolt negatív hatások minimalizálása érdekében, különösen a vaddisznó és a legelő haszonállatok esetében, de a mérsékelt jótékony hatások (pl. zsákmánybázisként) fenntartása is alapvető szempont.

A terepi kutatásaink elsősorban a csülkös vadfajok hatásait vizsgálták a fokozottan védett kaszpi haragossikló (*Dolichophis caspius*) városi élőhelyén, Budapesten, Vöröskőváron. Itt egy 3,2 ha-os területet mértünk fel, ahol a becserjésedés egy komoly veszélyeztető tényező. Vizsgálatunk integrált módszertani megközelítést követett.

1) Megvizsgáltuk a növényzet borításának időbeli változásait a vizsgált területen terepi megfigyelések és pilóta nélküli légi rendszerek (UAS) segítségével. Ennek során Phantom 4.0 drónnal légifelvételeket készítettünk, és a képeket Dronedeploy alkalmazás segítségével ortomozaikká alakítottuk, majd az ortomozaikból digitalizáltuk a cserjéket, és kiszámítottuk a cserjék által lefedett területet és a cserjesűrűséget a 20x20 m-es rácscellákban.

2) Nyomon követtük a csülkös vadfajok hatását a becserjésedés folyamatára a fásszárú fajokon és facsemetéken történő vadrágás és a vaddisznó túrásain keresztül. Ezért havonta gyűjtöttük a megtúrt foltok GPS-adatait a 20x20 m-es rácscellákban (n=81), és terepi megfigyelésekkel becsültük meg a megtúrt felület kiterjedését és az egyes cellákban elérhető fás növényzetet. Ezzel párhuzamosan felmértük a szarvasfélék rágása és a növényi táplálékkínálat közötti összefüggést egy speciális, 50x50x30 cm-es fakeret használatával, melyben a mintapontokon megszámoltuk a rendelkezésre álló és a megrágott fás hajtások számát egy 1 km-es felvételezési szakaszos mentén.

3) Vizsgáltuk a kaszpi haragossikló preferenciáját az egyes élőhelyfoltokra a vizsgált területen rögzített területhasználatuk alapján. Rádiótelemetriás vizsgálattal követtünk nyomon öt kifejlett kígyót, és elemeztük a mikroélőhely-preferenciáikat, mozgáskörzetük méretét és napi elmozdulásaikat.

4) Mindemellett megvizsgáltuk a lehetséges közvetlen emberi és ragadozó hatásokat a kaszpi haragossiklóra. Ehhez a kígyók búvóhelyeinél kameracsapdákat helyeztünk ki. Ezenkívül a kaszpi haragossiklóra gyakorolt közvetlen emberi hatásokat egy 1,5 méteres, kaszpi haragossiklót utánzó műanyag kígyó gyalogösvényre kihelyezésével is megvizsgáltuk, és feljegyeztük az emberek és a sétáltatott kutyáik reakcióit.

A területen végzett cserjeborítás becslésére irányuló vizsgálatunk azt mutatta, hogy a cellák 51%-át 45%-nál kevesebb cserje borította (0-40%), ami arra utal, hogy a cserjék között néhány nyílt folt is elérhető. Ez heterogén élőhelyet eredményez, amely alkalmasabb a haragossiklók számára. Eredményeink szerint a jobban megtúrt cellákban kevesebb volt a csemete, és több a kevésbé feltúrtakban, bár a különböző cserjesűrűségű területeken nem volt szignifikáns különbség a csemeték számában. Azt is kimutattuk, hogy a vadrágás sokkal kevésbé befolyásolja a becserjésedés folyamatát a területen. Jacobs preferencia index számításaink azt jelezték, hogy a legtöbb fajt elkerülik a szarvasok, és a vadrágás több mint fele a domináns fajon, nevezetesen a galagonyán (*Crataegus monogyna*) történt.

A kaszpi haragossiklók területhasználatának vizsgálata alapján a kígyók intenzíven használták a fás növényzettel borított területeket, ahol magas a megfelelő búvóhelyek, telelőhelyek elérhetősége. A jelölt haragossiklók a tavasztól őszig terjedő aktivitási időszakban a vizsgálati terület 40,15 ha-nyi részén belül mozogtak, de télre visszahúzódtak a telelőüregekben bővelkedő, 1,75 ha-os központi területre. Az aktív periódusuk során az egyedek mozgáskörzet mérete 6,1 és 15,5 ha között változott, a minimum konvex poligon (MCP) módszerrel becsülve. Ehhez képest az adaptív kernel módszer adta a legmagasabb átlagot (13,8 ha), míg a LoCoH-R alapján kaptuk a legkisebb mozgáskörzet méreteket (5,19 ha). Megállapítottuk, hogy a fő aktivitási időszakban az egyedek átlagos napi elmozdulása 12,6 és 36,6 m között alakult.

A vadkamerás felvételeken a kaszpi haragossikló rejtekhelyeinél vaddisznót vagy más csülkösvadat nem tudtunk kimutatni, csak egy vörös rókát (*Vulpes vulpes*) észleltünk. Amikor azonban az ember és a kaszpi haragossiklók közötti direkt kölcsönhatásokat vizsgáltuk, akkor a hatások erőteljesebbnek mutatkoztak. Mindösszesen 40 kerékpáros, 22 kocogó és 163 gyalogos eseményeit rögzítettük. A kerékpárosok 77%-a (n = 31) ütötte el a kígyót, 23%-a (n = 9) pedig elment mellette, vagy ráfordult, de nem állt meg. A kocogók a kígyót az esetek 36%-ában (n = 8) vették észre, de az esetek 64%-ában (n = 14) nem. Minden kocogó, aki észrevette, megállt, hogy a műkígyót megfigyelje. A tanösvényen a leggyakoribb tevékenység a gyaloglás volt. A gyalogosok a műkígyót az esetek 87%-ában (n = 142) vették észre. Ez a 142 ember megállt, hogy megfigyelje a kígyót. Sok esetben azonban nem voltak tudatában annak, hogy ez egy álkígyó. Az esetek 9%-ában (n = 15) a sétálók elmenekültek a kígyótól. Olyan alkalmakkor (n = 3), amikor az emberek egy csoportban sétáltak, mindig ráléptek a műkígyóra. De a legtöbb esetben a szabadon sétáltatott kutyák támadták meg a műkígyót.

A kaszpi haragossikló elszigetelt populációjának fennmaradása mindenekelőtt azt jelezheti, hogy a városkörnyéki ökoszisztéma még viszonylag jó természetességi állapotban van. Mivel azonban eredményeink azt bizonyítják, hogy a patások önmagukban nem állíthatják meg hatékonyan a becserjésedés intenzív folyamatát, a területen szükségesek a kezelési beavatkozások. Egyrészt fontos a vaddisznópopuláció monitorozása, mivel túrási aktivitásuk fontos szerepet játszhat a haragossikló élőhelyén a nyílt foltok fenntartásában, a becserjésedés lassításában, azonban direkt kedvezőtlen hatásaik is lehetnek a hüllőkre az elfogyasztásukkal. Emellett a cserjeirtás emberi munkaerővel is megoldandó az élőhely heterogenitásának megőrzése érdekében.

10. 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*). 6th European Congress for Conservation Biology. 22 – 26 August 2022.

Other publications

- Conference Article

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- Contributing Author: Book Chapter

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12. APPENDICES

Appendix A: Bibliography

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Appendix B: List of ungulate and reptile species (common and Latin name) mentioned in the scientific papers. Each ungulate is paired with reptile it has impacted and vice versa. Type of the reported impact (kind of ungulate activity and whether direct or indirect and positive or negative to reptiles) and the papers publishing them are demonstrated. “- - “= Impact on reptiles in general not on a specific species, “- “= Negative impact, “+” = Positive impact. IUCN Conservation status: Least Concern $^{(LC)}$, Endangered $^{(EN)}$, Critically Endangered $^{(CR)}$, Vulnerable $^{(VU)}$, Data deficient $^{(DD)}$ and Near Threatened $^{(NT)}$.

Ungulate species **(latin name)**	**Ungulate species** **(Common name)**	**Reptile species** **(latin name)**	**Reptile species (common name)**	**Type of** **impact**	**+/-**	**Number of times pairs mentioned in publications**	**Authors**
Axis axis	Chital deer	Lacerta viridis^{LC}	Green lizard	(Indirect) **Grazing** – deer removes understorey (habitat) of lizards	-	1	Mohanty et al., 2016
Bos taurus	Cattle	*Centrochelys sulcata*^{EN}	African spurred tortoise	(Indirect) **Grazing** – cattle reduce food for spurred tortoise	-	1	Petrozzi et al., 2018
Bos taurus	Cattle	*Clemmys muhlenbergii*^{CR}	Bog turtle	(Indirect) **Grazing** – cattle remove cover for turtles	-	1	Tesauro and Ehrenfeld, 2007
Bos taurus	Cattle	*Iguana iguana*^{LC}; *Lygodactylus sp.*^{LC} *and Tiliqua scincoides*^{LC}; *Phrynosoma platyrhinos*^{LC}	Green iguana; Dwarf gecko and Common blue-tongued skink; Desert horned lizard	(Indirect) **Competition** (interference) – for space-use between reptiles and cattles	-	3	Mitchell, 1999; Neilly et al., 2018; Newbold and Macmahon, 2008
Capra hircus	Domestic goat	*Hemidactylus turcicus*^{LC}	Mediterranean house gecko	(Indirect) **Grazing –** goat removes understorey/cover (habitat)	-	1	Pafilis et al., 2013

Ungulate species (latin name)	Ungulate species (Common name)	Reptile species (latin name)	Reptile species (common name)	Type of impact	+/-	Number of times pairs mentioned in publications	Authors
Equus asinus	Feral burro	*Gopherus agassizii*^{CR}	Mojave Desert tortoise	(Indirect) **Grazing** – overgrazing by abundant burros reduce population density of tortoises	-	1	Berry et al., 2020
Kobus kob	Kob	*Python sebae*^{NT}	African rock python	(Direct) **Predation** – python feeds on kob as prey	+	1	Antwi et al., 2019
Loxodonta africana	African elephant	*Lygodactylus. spp.*^{LC} *and Tiliqua scincoides*^{LC}	Dwarf gecko and Common bluetongue skink	(Indirect) **Grazing** – bare soil after grazing increases mortality for gecko and skink	-	2	Gordons et al., 2021; Nasseri et al., 2011
Odocoileus virginianus	White-tailed deer	*Python bivittatus*^{VU}	Burmese python	(Direct) **Predation** – deer as prey for python (remains of 3 deers in stomach of the python)	+	2	Boback et al., 2016; Boback et al., 2020
Odocoileus virginianus	White tailed deer	*Thamnophis sirtalis*^{LC}	Common garter snake	(Indirect) **Presence** – ungulates increase abundance of garter snakes through augmenting their invertebrate prey density	+	1	Greenwald et al., 2008
Ovis aries *and* *Bos taurus*	Sheep and Cattle	*Carlia tetradactyla*^{LC}, *Morethia boulengeri*^{LC} *and Ctenotus spaldingi*^{LC}	Southern rainbow-skink, Boulenger's snake-eyed skink and Straight-browed ctenotus	(Indirect) **Grazing** – sheep and cattle remove cover for the skinks	+	1	Kay et al., 2017

Ungulate species **(latin name)**	**Ungulate species** **(Common name)**	**Reptile species** **(latin name)**	**Reptile species (common name)**	**Type of** **impact**	**+/-**	**Number of times pairs mentioned in publications**	**Authors**
Ovis aries *and* *Bos taurus*	Sheep and Cattle	*Cryptoblepharus pannosus*^{LC}, *Hemiergis talbingoensis*^{LC}, *Christinus marmoratus*^{LC}	Ragged snake-eyed skink, Victoria three-toed earless skink and Marbled gecko	(Indirect) **Grazing** – sheep and cattle remove cover for the skinks	-	1	Kay et al., 2017
Ovis aries	Domestic sheep	*Lacerta viridis*^{LC}	Green lizard	(Indirect) **Grazing** – sheep removes cover for the lizards	-	1	Smith et al., 1996
Ovis aries	Domestic sheep	*Tiliqua adelaidensis*^{EN}	Pygmy bluetongue lizard	(Indirect) **Grazing** – sheep removes cover for the lizards	-	3	Brown et al, 2011; Kazmaier, 2001; Nielsen and Bull, 2016
Sus scrofa	Wild boar	*Alligator mississippiensis*^{LC}	American alligator	(Direct) **Predation** – nest predated by wild boar	-	2	Campos and Mourão, 2014; Elsey et al. 2012
Sus scrofa	Wild boar	*Anolis carolinensis*^{LC}, *Storeria occipitomaculata*^{LC} *and Sceloporus undulatus*^{LC}	Green anole, Red-bellied snake and Eastern fence lizard	(Direct) **Predation** – reptile species as prey for wild boar	-	1	Jolley et al., 2010
Sus scrofa	Wild boar	*Blanus cinereus*^{LC} *and Psammodromus algirus*^{LC}	Iberian worm lizard and Algerian sand racer	(Direct) **Predation** – reptile remains found in stomach content of wild boar	-	2	Abáigar, 1993; Briedermann, 1976
Sus scrofa	Wild boar	*Chelodina longicollis*^{NT}	Eastern long-necked turtle	(Indirect) **Rooting, Trampling** – wild boar destroys turtle's habitat	-	1	Doupé et al., 2009
Sus scrofa	Wild boar	*Chelodina rugosa Ogilby*^{NT}	Northern snake-necked turtle	(Direct)	-	2	Fordham et al., 2006 and 2008

				Predation – wild boar kills turtles			
Ungulate species (latin name)	**Ungulate species (Common name)**	**Reptile species (latin name)**	**Reptile species (common name)**	**Type of impact**	**+/-**	**Number of times pairs mentioned in publications**	**Authors**
Sus scrofa	Wild boar	*Malpolon monspessulanus*^{LC}	Montpellier snake	(Direct) **Predation** - Montpellier snake as prey for wild boar	-	1	Ballouard et al., 2021
Sus scrofa	Wild boar	*Chelonia mydas*^{EN}	Green sea turtle	(Direct) **Predation** – sea turtle as prey for wild boar	-	2	Engeman et al., 2019; Nordberg et al., 2019
Sus scrofa	Wild boar	*Geochelone elephantopus*^{EN}	Galápagos giant tortoise	(Direct) **Predation** – wild boar killed adult tortoises	-	1	MacFarland et al., 1974
Sus scrofa	Wild boar	*Kinosternon hirtipes*^{LC}	Rough-footed mud turtle	(Direct) **Predation** – turtle as prey for wild boar	-	1	Platt et al., 2019
Sus scrofa	Wild boar	*Natator depressus*^{DD}, *Lepidochelys olivacea*^{VU} *and Eretmochelys imbricata*^{EN}	Flatback turtle, Olive ridley turtle and Hawksbill turtle	(Direct) **Predation** – turtle nests predated by wild boar	-	1	Whytlaw et al., 2013
Sus scrofa	Wild boar	*Natrix natrix*^{LC}	Grass snake	(Direct) **Predation** – snake remains found in stomach content of wild boar	-	1	Tucak, 1996
Sus scrofa	Wild boar	*Storeria occipitomaculata*^{LC}	Red-bellied snake	(Direct) **Predation** – snake remains found in stomach content of wild boar	-	1	Scott, 1973
Sus scrofa	Wild boar	*Testudo hermanni*^{NT}	Hermann's tortoise	(Direct) **Predation** – tortoise remains found in	-	1	Vilardell et al., 2012

				stomach content of wild boar			
Ungulate species (latin name)	**Ungulate species (Common name)**	**Reptile species (latin name)**	**Reptile species (common name)**	**Type of impact**	**+/-**	**Number of times pairs mentioned in publications**	**Authors**
Sus scrofa	Wild boar	*Tropidurus jacobii*^{LC} *and Pseudalsophis steindachneri*^{NT}	Santiago lava lizard and Painted racer	(Direct) **Predation** – reptile remains found in the stomach content of wild boar	-	1	Coblentz and Baber, 1987
Sus scrofa	Wild boar	*Varanus komodoensis*^{EN}	Komodo dragon	(Direct) **Predation** – wild boar providing prey to dragon	+	3	Ariefiandy et al., 2020; Jessop et al., 2019 and 2020
Sus scrofa	Wild boar	*Vipera berus*^{LC}	Common European viper	(Indirect) **Rooting** – wild boar foraging behaviour reduces common viper abundance in the area	-	1	Graitson et al., 2019
Tapirus terrestris^{VU}	Lowland tapir	*Chelonoidis denticulata*^{VU}	Yellow-footed tortoise	(Direct) **Predation** – tortoise as prey for tapir	-	1	Edison and David, 2020