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Research article

Before-after-control-impact field experiment shows anti-predator netting enhances occupancy of the threatened Hungarian meadow viper (*Vipera ursinii rakosiensis*)

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The Hungarian meadow viper is an endangered grassland-dwelling species, which faces high predation pressure, partially due to avian species that forage in its habitat. Predation pressure by avian predators is caused not only by abundant game species (e.g. hooded crow, *Corvus cornix*) but also by protected and threatened species (e.g. short-toed eagle, *Circus gallicus*; common buzzard, *Buteo buteo*; roller, *Coracias gar-rulus*) in the project area (Felső-kiskunsági turjánvidék, Hungary). Mark-recapture data of a reintroduced viper population showed a very low, 42% yearly average apparent survival rate. To establish a strong sub-population we applied anti-predator netting (APN) by building a 200 × 200 × 3 m (4 ha) totally closed exclusion site with a mesh net, lateral sides boosted with a 1 m high steel field fence to exclude mammals as well as birds. To test the effect of APN we monitored viper occupancy at 50 × 50 m sampling plots in a before–after/control–intervention (BACI) design, where we randomly placed quadrats 0.25 ha (50 × 50 m) to be surveyed, n = 26 at control habitats and n = 4 below the APN enclosure. We collected data across four years (2020–2023), in each year during the spring by 10 surveys replicates in each plot resulting in 1200 surveys to record viper detection/non-detection data. We applied a multi-season occupancy model to estimate site occupancy changes to test the effects of the BACI design. Occupancy probabilities were increasing during the four consecutive survey years in both the control and the intervention sites, however except for the initial occupancy, the occupancy probability became significantly higher at APN sites, and the APN intervention had a significant positive effect on viper occupancy, while the distance to APN showed negative effect. Predator exclusion is an effective method to minimise

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predation pressure and potentially has a deterministic positive demographic outcome, however, due to the high logistical and maintenance costs, this measure can be applied at only a few sites.

Keywords: occupancy modelling, predation exclusion, reptile management, species conservation, species recovery

Introduction

Predation is a natural process that can significantly affect the distribution, abundance, and behaviour of prey populations (Nelson et al. 2004). Even though its effects are often overlooked, when predation pressures become too high or the prey populations become small due to other factors, they can significantly decline populations of vulnerable or endangered prey species (Schneider 2001). Anthropogenic factors such as habitat degradation, fragmentation, and changes in the trophic network can exacerbate predation pressures (Soulé et al. 1988). Threatened species are particularly susceptible to predation due to their small population sizes, restricted distributions, and limited genetic diversity (Caughley and Sinclair 1994). Understanding the factors that drive predation pressures and developing effective strategies to manage them is essential for biodiversity conservation and ecosystem balance if trophic networks change due to anthropogenic pressure.

In the case of some threatened species or populations, effective measures to mitigate the impact of predation are needed to promote their survival and recovery (Dirzo et al. 2014). These measures may include habitat restoration to promote population growth through enhanced carrying capacity or provide better shelters, predator control, or predator exclusion techniques. Effective measures to manage predation pressures include lethal and non-lethal methods. Lethal methods such as hunting and trapping can reduce predator populations and could be necessary to protect livestock or individuals of endangered prey species, however, they can also have unintended consequences such as disrupting ecosystem dynamics or bycatch of protected predators (Conover 2001).

Non-lethal methods such as habitat management, predator exclusion, and the use of deterrents offer more sustainable solutions compared to continuous trapping or hunting (Tanentzap and Lloyd 2017). Habitat management, such as restoring or enhancing habitat quality, can increase the availability of resources for prey species and decrease the vulnerability of individuals to predation (Landis et al. 2000). The promotion of microhabitats, have been shown to provide more suitable biotic and abiotic conditions, including hydric and thermic factors, reducing predation pressure on vipers, as microhabitat quality modulate predation risks because non-linear, highly structured habitat elements, predation pressure by mammals and birds can be hindered (Hansen et al. 2019, Worthington-Hill and Gill 2019, Duchesne et al. 2022). Predator exclusion methods such as fencing, netting, or electric shock devices can be effective in preventing access to vulnerable areas (Smith et al. 2020). The use of deterrents such as sound or light devices may also be effective in repelling predators from vulnerable

species (Cassidy 2015). Anti-predator netting (APN) is a rarely used specific form of predator exclusion that has been shown to be effective in protecting threatened species by the creation of predator-fenced sanctuaries (Innes et al. 2012). However, the effectiveness of these methods may vary depending on the predator species, habitat, and local conditions (Scofield et al. 2011, Bendell 2015), while it can be also influenced by the dispersal ability and home range of the prey species.

The Hungarian meadow viper *Vipera ursinii rakosiensis* is a subspecies of the meadow viper *Vipera ursinii* near extinction (Péchy et al. 2015), listed as an endangered taxon in the IUCN red list (European Reptile and Amphibian Specialist Group 1996). In the last two decades, huge conservation efforts and significant improvements have been implemented to enhance the long-term survival of Hungarian meadow vipers in Hungary. Since 2004, the conservation of the remaining viper populations has been carried out within the framework of LIFE projects, which have increased the extent of habitats (Péchy et al. 2015, Mizsei et al. 2020), implemented viper-friendly grassland management in several areas, and either reinforced declining populations with individuals from ex situ breeding or restored extinct populations (Péchy et al. 2015). Despite the conservation interventions, the monitoring of LIFE projects between 2004–2013 did not detect the growth of population size or increase in density at the largest populations of Hungarian meadow vipers in Kiskunság and is still certainly lower than the historical density (Móré et al. 2022).

Most likely, the main factor causing the seemingly stagnate population size of the Hungarian meadow viper is the high and growing predation pressure by generalist predators (Móré et al. 2022). In 2019, a third LIFE project was launched with the aim of reducing predation pressure on the Hungarian meadow viper population in the Pannonian basin. This project also includes goals related to habitat restoration, habitat connectivity isolated habitats, ex situ breeding, and releasing head-started snakes. One of the actions of the project is the building of a large, 4 ha totally closed APN enclosure to protect viper individuals from mammal and bird predation. In this study, we are assessing the effectiveness of the intervention using before–after control–intervention (BACI) sampling design and occupancy modelling accounting for the detection probability of Hungarian meadow viper. We expect that the application of APN will increase viper occupancy at the safeguarded site compared to control sites and to the baseline surveys. We also expect that control sites near the APN will show increased occupancy due to the dispersal of vipers from the APN enclosure because the site should function as a predator-free source subpopulation where the offspring survival rate is high.

Material and methods

Study species

The Hungarian meadow viper *V. u. rakosiensis* is one of Europe's most endangered vertebrates. This grassland specialist venomous snake was historically common in the meadows and sandy or loess grasslands of the Vienna Basin, around Lake Fertő, Hanság region, around Budapest, the Kiskunság region and the surroundings of Cluj-Napoca in the Transylvanian Plain (Mizsei et al. 2018). As a result of the conversion of majority of grassland habitats to plough-lands, the Hungarian meadow viper has disappeared from much of its range and the remaining populations have been significantly reduced in numbers, due to intensive use of grassland habitats and other threatening factors (Péchy et al. 2015, Mórét al. 2022). Currently, less than 10 isolated populations are known today in the Hanság, Kiskunság and Transylvanian Plain areas (Mizsei et al. 2018). The Hungarian meadow viper is preyed upon by native predators like the European badger *Meles meles*, the red fox *Vulpes vulpes* and several avian predators like the common buzzard *Buteo buteo* (Mórét al. 2022).

Anti-predator netting

To protect Hungarian meadow viper individuals from predators, we built a 0.2×0.2 km (4 ha) APN, using 3 and 4 m long wooden poles placed in alternating rows in a 10×10 m grid (Fig. 1). We fitted a polyamide mesh net (thread of 2 mm, by a mesh gap of 50×50 mm in 10×100 m bolts) at a 2.3–3.3 m ceiling height on a 4 mm steel wire rope underpinning fitted on the wooden poles. Later sides of the APN were made by the same type of mesh net, boosted with a 1 m high steel field fence gradually denser weave (Fig. 1). The construction of the APN

site began in September of 2020, and the system became fully functioning in March of 2021.

Sampling design

The sampling areas were designated in grassland patches of the HUKN20003 Felső-kiskunsági Turjánvidék Natura 2000 SCI priority conservation area of the Kiskunság National Park Directorate (Fig. 2). To test the effect of APN we used a BACI design. For control, we selected grassland habitats managed by livestock grazing similarly as the APN enclosure, where we randomly placed quadrats 0.25 ha (50×50 m) to be surveyed, $n=26$ at control habitats and $n=4$ at the APN enclosure (Fig. 2).

Data collection

We surveyed the sampling quadrats for Hungarian meadow viper observations in four consecutive survey years (primary surveys), during spring (25 March–15 May) between 2020–2023. All quadrats were surveyed 10 times in each season between 7:00 am and 6:00 pm h (secondary surveys). The quadrats were surveyed by walking along east-west oriented straight lines located 10 m apart from each other, which resulted in a total surveyed distance of ~ 300 m per quadrat per occasion. During secondary surveys, the surveyor walked slowly (~ 2 km h^{-1}), stopping at least every five paces and looking around for viper individuals or shed skins. Survey duration varied from 5 to 30 min, depending on the number of records and habitat complexity, with longer surveys conducted in denser vegetation. Additional to visual surveys, the quadrats were surveyed at least once in each survey season except for the first survey season in 2020, by a conservation detection dog (CDD) unit trained for Hungarian meadow viper detection. We recorded the GPS position, time and

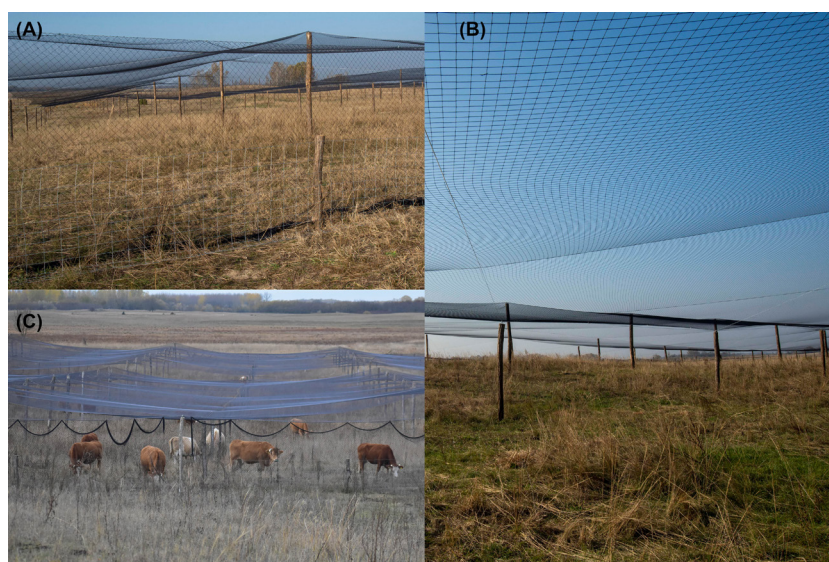


Figure 1. Photos of the APN site. The APN was made by the mesh net, boosted with a 1 m high steel field fence (A, B, pictures by E. Mizsei). The ceiling height allows for grassland management (C, picture by V. Schneider).

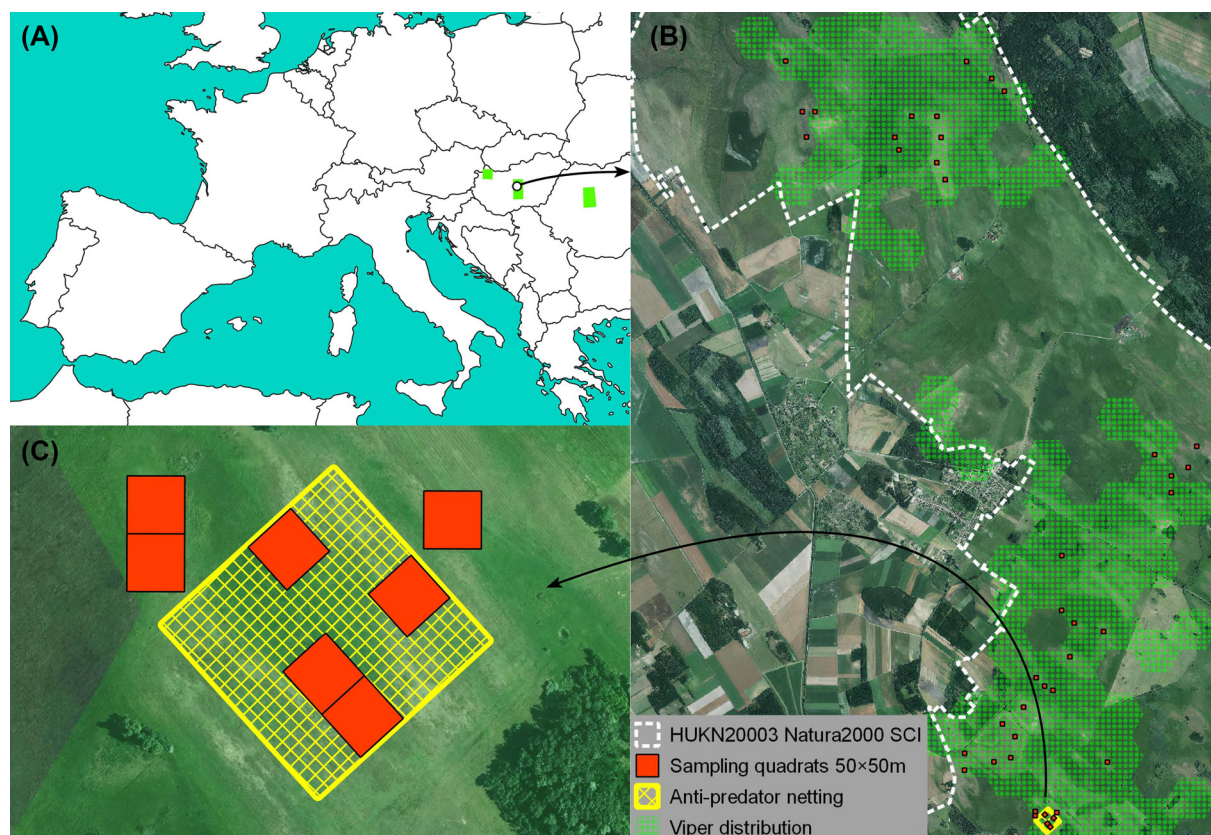


Figure 2. The spatial extent of sampling. Distribution of *Vipera ursinii rakosiensis* modified from Mizsei et al. (2018): the green squares show the distribution of *V. u. rakosiensis* at the scale of a 50×50 km grid, and the study area is marked by a white point (A). The location of the APN site and the location of 50×50 m sampling quadrats (B). Close-up of the APN site and surrounding sampling quadrats (C).

individual data (i.e. sex, age, activity, scalation pattern for further identification not analysed here) of detected vipers for further research in the OpenBioMaps mobile application (Bán et al. 2022), including the metadata of the survey (start and end time, tracklog, surveyor id).

As temperature fundamentally influences the activity of reptiles, to model detection probability we measured operative temperature during the surveys. Operative temperature is the environmental temperature that is available to an individual at different times during thermoregulation (Shine and Kearney 2001). Operative temperature cannot be calculated from commonly measured meteorological data because it is influenced by radiation, surface temperature, wind speed, humidity, animal shape and heat absorption, in addition to most available air temperature (Kearney and Porter 2020). To measure operative temperature, we used $n=8$ thermometers (BTP-06 temperature sensors connected to a BEL-06 ecologger unit, Boreas Ltd., Hungary) placed in copper tubes painted to mimic the viper's pattern, $n=4$ placed in full sun and $n=4$ placed in a half-shade of grass. The logger recorded the operative temperature values at 2 min intervals.

To test the effect of distance from the APN site on viper occupancy, we calculated the distance to the APN site of each sampling quadrat using the QGIS 3.14 distance matrix function calculated in EPSG:23700 projection in meters.

Statistical analysis

Given the very low encounter rate of the Hungarian meadow viper due to its cryptic lifestyle and camouflage colouration it is fundamental to use analytical methods that consider the detectability of the species of interest. We applied multiseason (dynamic) occupancy models (MSOM) to estimate changes in site occupancy related to APN conservation intervention and detectability based on repeated secondary surveys conducted in consecutive primary survey seasons. MSOMs are developed to provide estimates of colonization and extinction between these primary survey seasons and to estimate changes in occupancy through time. Detection probability was estimated based on the detection/non-detection data from individual secondary surveys, which was used to estimate initial site occupancy combined with observed occupancy. Subsequently, colonization and extinction parameters were estimated based on changes in estimated occupancy from initial occupancy estimates that occur between primary survey seasons.

We prepared and formatted the data of the surveys using the functions of the 'hunviphab' package (Mizsei 2022). We built MSOMs (MacKenzie et al. 2003) in a Bayesian framework using the package 'unmarked' (Fiske and Chandler 2011) and 'ubms' (Kellner et al. 2021). We used model

selection based on LOOIC (leave-one-out cross-validation (LOO) information criterion) values (Vasishth et al. 2018). In the model candidates, the explanatory variables in the detection (p) submodel were the mean of the operative temperature during the survey replicates and surveyor ID as a factor variable, while in the occupancy (state) submodel for initial occupancy (ψ) we included the control/impact and the distance to APN variables to assess the potential differences in occupancy before building the APN. For colonization (γ) and extinction (ϵ) submodels we included the distance to APN and years since building the APN as explanatory variables. We performed a posterior predictive check on the models using the goodness-of-fit test using the MacKenzie-Bailey χ^2 test of the 'ubms' package (Kellner et al. 2021).

All data processing and analysis were conducted in the R statistical environment (R ver. 4.1.3, www.r-project.org).

Results

During the surveys, we recorded $n=37$ Hungarian meadow vipers: in 2020 we detected $n=7$ vipers in control and $n=0$ in APN sampling quadrats, in 2021 we detected $n=2$ vipers in control and $n=3$ in APN sampling quadrats, in 2022 we detected $n=11$ vipers in control and $n=1$ in APN sampling quadrats and in 2023 we detected $n=9$ vipers in control and $n=4$ in APN sampling quadrats (Fig. 3). Out of the $n=30$ sampling quadrats we detected the occupancy of the Hungarian meadow viper in $n=19$ quadrats (Fig. 3), thus the naive occupancy was 0.6 across the sampling seasons.

The model selection performed on MSOMs revealed as best model the candidate which were constructed with the explanatory variables of control-impact in the initial occupancy (ψ) submodel, distance to APN, years since APN and their interaction in the colonization (γ) and extinction (ϵ) submodels, and temperature and surveyor ID in the

detection (p) submodel (Table 1). The MSOM goodness-of-fit test revealed that the fitted model did not deviate from the simulated dataset ($\chi^2=1147.5$, $p=0.422$, Table 1).

Posterior distributions of the effect and the response curves of explanatory variables of the best model showed no difference in initial occupancy among control and APN sites (before the building the APN), however, the estimated occupancy was lower at the sites designated for APN (Fig. 4–5). Distance to APN had negative effect on colonization and positive effect on extinction probability, the years since building the APN showed positive effect on colonization and negative effect on extinction probability on viper occupancy, while the interaction of these variables showed positive influence on colonization and negative influence on extinction probability (Fig. 4–5). Operative temperature had a negative influence on detection probability (Fig. 4–5), while out of the 28 surveyors, five had positive influence on detection probability, including the CDD unit. The mean of the estimated occupancy across primary survey seasons was 0.286 ± 0.032 ($\pm$ SE), and the mean detection probability of the Hungarian meadow viper was 0.122 ± 0.003 ($\pm$ SE) across secondary surveys. Estimated viper occupancy became significantly higher at the APN sites compared to the control sites after the second year following the building of the APN (Fig. 6).

Discussion

Our study aimed to evaluate the effectiveness of APN in protecting Hungarian meadow vipers from bird and mammal predators. We expected that the application of APN would increase viper occupancy significantly at the safeguarded site compared to control sites and to the baseline surveys. We also expected that control sites near the APN will show increased occupancy due to the dispersal of vipers from the APN

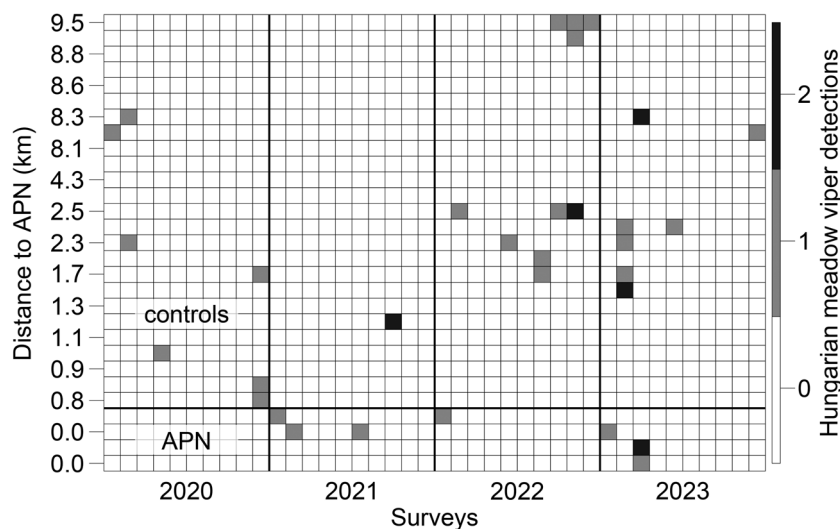


Figure 3. *Vipera ursinii rakosiensis* detections during the surveys, ordered by the sequence of surveys and the distance of sampling quadrat centroids from the center of the APN site.

Table 1. Model selection of multiseason (dynamic) occupancy models ranked by LOOIC values, and the results of GOF test of model candidates

Model	Variables included in the submodels				MacKenzie-Bailey GOF test		
	Initial occupancy (ψ)	Colonization (γ)	Extinction (ϵ)	Detection (p)	LOOIC	χ^2	p
1	Controll-intervention	Distance to APN years since APN distance:year	Distance to APN years since APN distance:year	Temperature observer	144.426	1147.5	0.422
2	–	Distance to APN	Distance to APN	Temperature	145.614	888.5	0.404
3	–	Distance to APN years since APN	Distance to APN years since APN	Temperature	147.293	1060.3	0.402
4	–	Years since APN	Years since APN	Temperature	151.533	1309.9	0.34
5	Controll-intervention distance to APN	Distance to APN years since APN distance:year	Distance to APN years since APN distance:year	Temperature observer	221.733	3361.9	0.078
6	–	–	–	–	221.866	3284.3	0.112

enclosure because the site should function as a predator-free source subpopulation where the offspring survival rate is high. Our findings show that the APN did indeed increase viper occupancy at the safeguarded site, consistent with our expectations. We found significant differences in occupancy between the control sites near the APN and the baseline surveys, suggesting the dispersion of vipers from the APN site.

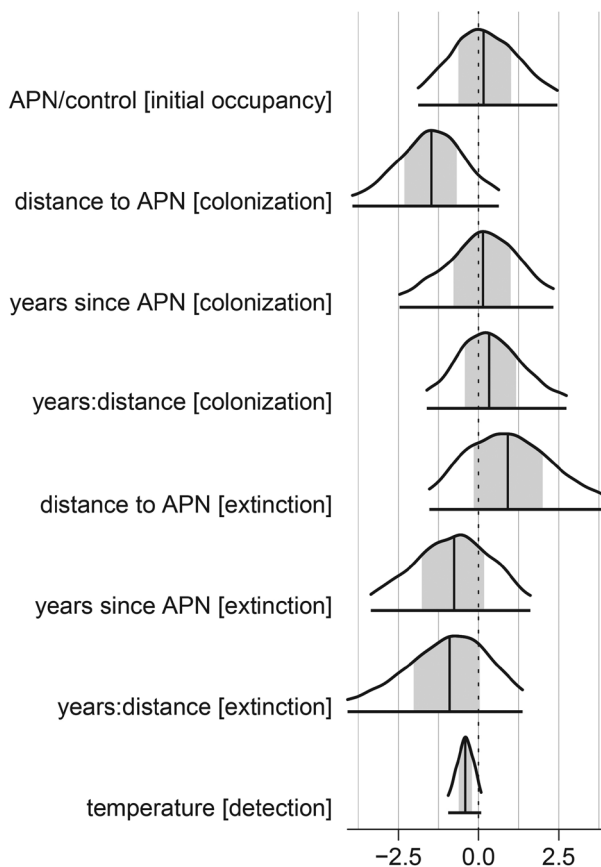


Figure 4. Posterior distributions for the variables influencing initial occupancy, colonization, extinction and detection of *Vipera ursinii rakosiensis* in the testing of APN intervention. Distribution curves represent the 95% credible interval, shaded areas represent the 50% credible interval and the vertical lines represent the mean effect size.

The results add to the growing body of literature on the effectiveness of predator exclusion methods in protecting vulnerable species and also contribute to the very limited literature on the effectiveness of APNs as a tool for predator exclusion. Studies with other types of fencing, such as the use of predator-exclusion cages to reduce predation of turtle nests, had found no negative impact on the nest environment or proxies for hatchling fitness (Riley and Litzgus 2013). Similarly, Smith et al. (2011) observed a significant increase in hatching success for bird populations with nest predation using exclusion fences or nest cages, highlighting the effectiveness of predator exclusion in enhancing the hatching success of vulnerable species. On the other hand, Reynolds and Tapper (1996) demonstrated the complexities associated with predator control, as changes in predator communities or predator-prey ratios can lead to increased predation losses. Additionally, Hayward and Kerley (2009) emphasized the ecological costs of fencing, including potential impacts on migration routes, biodiversity range use, overabundance, inbreeding, and isolation. In comparison with these findings, our results indicate that short-term predator exclusion has a deterministic positive effect on Hungarian meadow viper occupancy potentially through a high individual survival rate, and we do not expect a negative impact on predator populations as we only fenced a 4 ha area in a near-to-12 000 ha grassland complex. However, changes in other prey populations like rodents are also likely to happen which can modify habitat quality in a non-intended direction, thus continuous monitoring is needed in the area (Burns 2011).

As the Hungarian meadow viper is an extremely cryptic snake, we choose a sampling and statistical framework to account for detectability. Thus, in addition to visual surveys, we employed a CDD unit to increase reptile detection probability. CDDs have been used successfully to detect a range of reptile species, including snakes, lizards, and turtles (Cablík et al. 2013). Furthermore, our study employed multi-season occupancy modelling to estimate site occupancy which accounts for the change in occupancy state between primary survey periods by estimating colonisation and extinction probability at the level of survey units.

One limitation of our study is the relatively small number of sampling sites, which may limit the generalizability of our

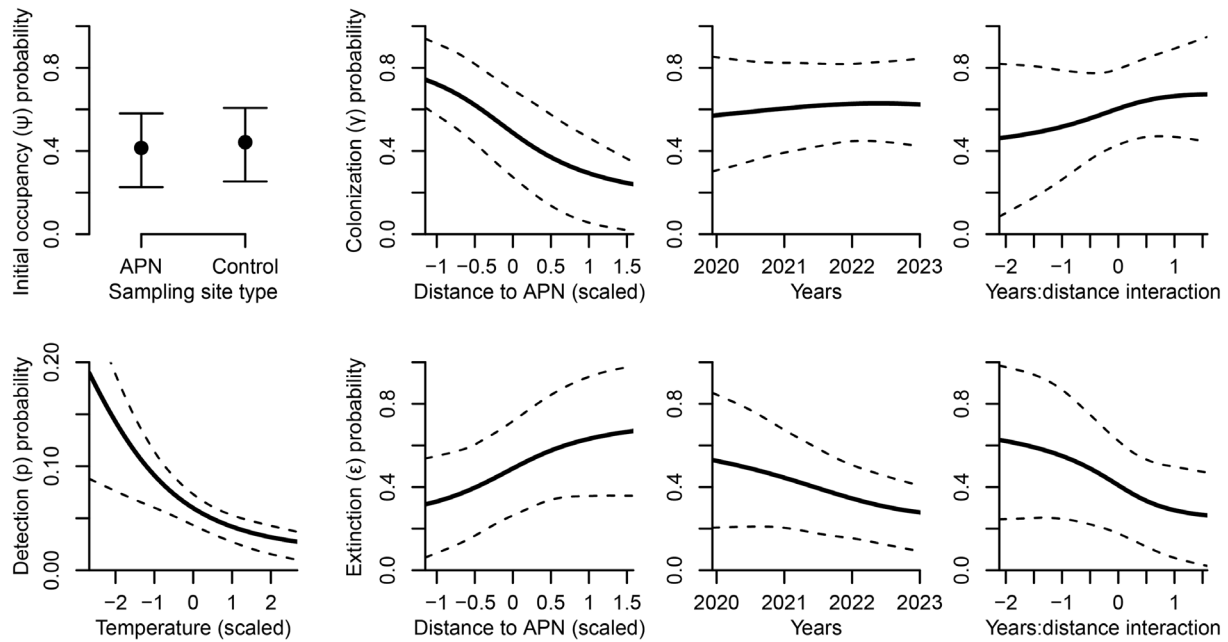


Figure 5. Marginal effects curves of the variables included in the occupancy model of *Vipera ursinii rakosiensis* for the testing of APN intervention. Lines show posterior means, while dashed lines represents the 95% credible intervals.

findings to other ecosystems or species, as the spatial replication of our APN intervention was limited to a single site. Furthermore, our study focused on a single threatened reptile species in a grassland habitat, which may limit the transferability. However, our study provides valuable evidence for the use of APNs as a tool for managing predation pressures on threatened reptile species. Future studies could evaluate the effectiveness of APNs across multiple sites to better understand the transferability of the method.

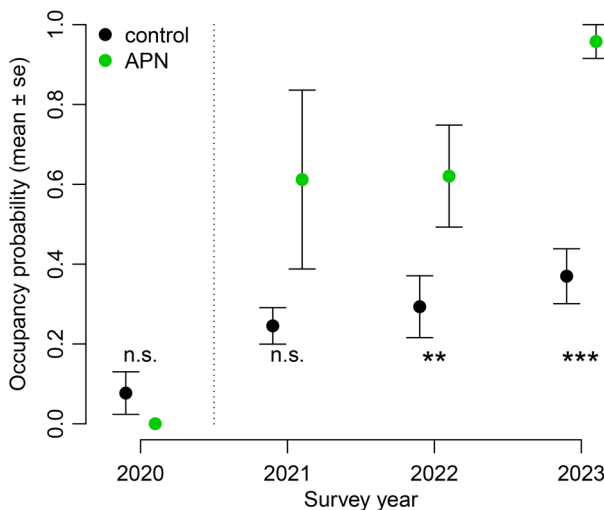


Figure 6. Occupancy estimates of the Hungarian meadow viper at the APN and control sites during the sampled years. Letters 'n.s.' indicate a non-significant difference in occupancy estimates between control and APN, while '**' indicate a significant difference lower than $p < 0.01$, and '***' indicate a significant difference lower than $p < 0.001$.

A further limitation of our study pertains to the closure assumption in site occupancy modelling, which assumes no colonization of unoccupied sites or extinction in occupied sites within the primary survey seasons (Kéry and Royle 2016). Our secondary surveys were conducted over a 50 day period, which raises the possibility of violating this assumption due to the movements or mortality of Hungarian meadow viper individuals. However, it is crucial to note that the closure assumption specifically applies to site occupancy rather than individual movements. Given the limited dispersal capacities documented in previous studies for this species (Újvári and Korsós 1997, Péchy et al. 2015), and based on the fact that multiple individuals contribute to site occupancy, we contend that the potential bias resulting from movements and mortality is unlikely to exert a significant influence on our findings.

There is one more potential source of bias, as we captured viper individuals before the building of the APN system to avoid mortality due to trampling and after the construction, we released them back. We designated the capture area by a 50 m buffer around the APN site including a patch of grassland between the closest dirt road resulting in a 9 ha area, and when we finished the construction works we released all the individuals ($n=23$) and the offspring of one gravid female captured ($n=22$) under the cover of the APN, thus we may have influenced viper density and occupancy at the APN site. However, if we check past monitoring data, the number of observed individuals in 2018 was $n=17$ at the study site, which is comparable to the number of captured individuals (Mizsei et al. 2020). This previous census data compared to the first primary survey when practically no vipers were observed at the APN site, highlights the fluctuation of viper occupancy before the exclusion of predators.

Our study provides a foundation for future research on the effectiveness of APN as a conservation tool for reptile species, which is needed to explore the long-term effects of APNs on predator populations and the ecological dynamics of the habitat. In addition, it would be valuable to conduct surveys over a longer time period to explore the demographic parameters of the threatened species, including individual survival, recruitment, and reproduction. Furthermore, expanding the spatial replication of APN interventions and exploring the effectiveness of APN in different ecosystems and with different predator and prey species could provide valuable insights into the generalizability of our findings.

Our study provides evidence that APN can effectively protect Hungarian meadow vipers from bird and mammal predators. While further research is needed to better understand the effectiveness of APNs in protecting vulnerable species and to address limitations in our study, our findings contribute to the growing body of literature on predator exclusion methods and highlight the importance of implementing effective conservation tools that could significantly promote the populations of the target species.

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Author contributions

Edvárd Mizsei: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Mátyás Budai:** Data curation (equal); Investigation (equal); Writing – original draft (equal). **Bálint Wenner:** Data curation (equal); Investigation (equal); Writing – original

draft (equal). **Gergő Rák:** Data curation (equal); Investigation (equal); Writing – original draft (equal). **Dávid Radovics:** Data curation (equal); Investigation (equal); Writing – review and editing (equal). **Barnabás Bancsik:** Data curation (equal); Investigation (equal); Writing – review and editing (equal). **Gergő Kovács:** Data curation (equal); Investigation (equal); Writing – review and editing (equal). **Ádám Tisza:** Data curation (equal); Investigation (equal); Writing – original draft (equal); Writing – review and editing (equal). **János Simics:** Data curation (equal); Investigation (equal); Writing – review and editing (equal). **Márton Szabolcs:** Data curation (equal); Investigation (equal); Writing – original draft (equal); **Csaba Vadász:** Conceptualization (equal); Funding acquisition (equal); Supervision (equal); Writing – review and editing (equal). **Attila Mór:** Conceptualization (equal); Data curation (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at <https://publons.com/publon/10.1002/wlb3.01147>.

Data availability statement

Data and code are available from the Zenodo Repository: <https://zenodo.org/records/10038019> (Mizsei et al. 2023).

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