

Population size and nocturnal activity of Cyprus Grass Snakes, *Natrix natrix moreotica* (Bedriaga, 1882), in an arid island environment

Marilena Stamatou^{1,2,*}, Giorgos Pishilis^{2,3}, Tariq Stark⁴ and Savvas Zotos^{1,2}

Abstract. Grass Snakes (*Natrix* spp.) constitute the most widespread snake taxon in the Eurasian continent. While research on Grass Snakes is historically robust, there is a lack of data for the distribution, population trends and estimates, and ecology of *Natrix natrix* inhabiting the island of Cyprus, often accredited on its elusive nature. The Grass Snake population in the Troodos Mountains has garnered the most attention in the past, while the vulnerable lowland population in the southeast of the island remains relatively understudied. It is assumed that this latter population is small, highly fragmented and inhabits habitats that face severe anthropogenic pressures. These threats are exacerbated by prolonged drought and heat waves. Population monitoring and estimates of the number of individuals per life stage are needed to inform and support the long-term conservation of lowland *N. natrix* populations in Cyprus. We estimated the number of individuals in two lowland areas and highlight the usefulness of nocturnal instead of diurnal transect surveys. Lastly, we recommend ways to move forward with monitoring the lowland population of the species in order to aid its long-term survival.

Keywords. Activity rhythm, Crepuscular, Daily Activity, Diurnal, Mediterranean Species, Monitoring, Population Estimation

Introduction

The Eastern Grass Snake, *Natrix natrix* (Linnaeus, 1758), is a rather common species with a wide Eurasian distribution (Speybroeck et al., 2020), ranging from northern and central Europe to the Mediterranean (including Cyprus) and into Asia (Fritz and Schmidler, 2020). Populations on Cyprus have been considered as the endemic subspecies *Natrix natrix cypriaca* (Baier et al., 2013; Nicolaou et al., 2014; Sparrow and Baier, 2016) and are protected as a priority species under the European Council Directive 92/43/EEC. Recent taxonomic insights revealed that *N. n. cypriaca* is a genetically impoverished recent invader on Cyprus,

taxonomically not distinct from the subspecies *N. n. moreotica* (occurring in western Anatolia and the southern Balkans), and proposed a refined intraspecific classification where *N. n. cypriaca* is a junior synonym of *N. n. moreotica* (Bedriaga, 1882) (Asztalos et al., 2021), which we use in the present paper. Cyprus constitutes one of the most southern localities and the highest end of the aridity spectrum of this subspecies (Asztalos et al., 2021). Compared to its counterparts elsewhere in Europe (Mertens, 1994; Conelli et al., 2011; Ayres, 2012; Norén and Åhlander, 2020), research on Grass Snake populations on Cyprus is still limited (Zotos et al., 2021, 2022; Stamatou, 2022).

In Cyprus, *N. natrix* are present within two regions of the island (Zotos et al., 2023). This concerns the Troodos Mountain Range (in the centre of the island), where they occur in and around streams and ponds, and the south-eastern lowlands where they occur within a system of ponds (Fig. 1). The area of the *N. natrix* population in the Troodos Mountain Range receives a relatively large amount of precipitation annually (600–1100mm, compared to the 320mm average for the whole island) with subsequent creation of numerous ephemeral streams and year-long water retaining ponds (Cleridou et al., 2014; Giannakopoulos et al., 2016). The lowland distribution of the species includes two distinct areas; Paralimni and Ayia Napa consist of dense urban

¹ Terrestrial Ecosystem Management Lab, Faculty of Pure and Applied Sciences, Open University of Cyprus, Giannou Kranidioti 33, Latsia 2220, Cyprus.

² Herpetological Society of Cyprus, P.O. Box 61435, Paphos 8134, Cyprus.

³ European University of Cyprus, Diogenes Str. 6, Engomi 2404, Nicosia, Cyprus.

⁴ Reptile, Amphibian & Fish Conservation Netherlands (RAVON), Toernooiveld 1, 6525 ED Nijmegen, Netherlands.

* Corresponding author. E-mail: marilenastamatou@outlook.com

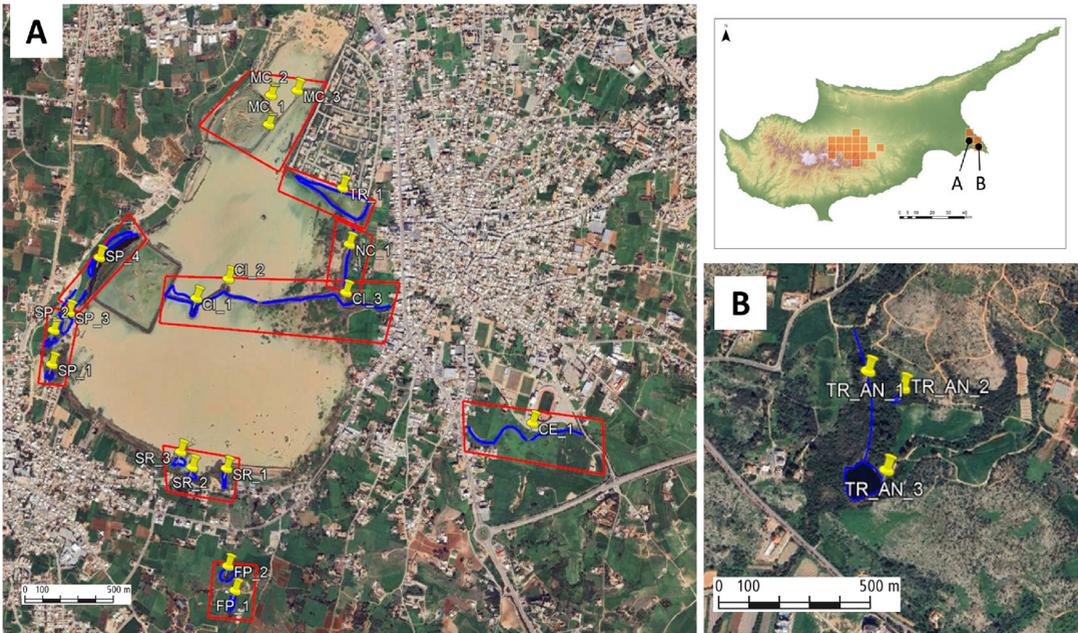


Figure 1. Map of the study area. Right up corner: Distribution of Grass Snakes in Cyprus (1x1 km grid). Data from www.herpatlas.cy. (A) Transects at the Paralimni area. (B) Transects at the Ayia Napa area. Yellow pins = start of the transect line. Blue lines = indication of water bodies. Red lines: rough indication of monitoring sites.

sprawl, separated by large patches of agricultural lands and roads with a high amount of traffic (Blosat 2002, 2005; Sophocleous and Nalbantis, 2017). The Grass Snake population in these lowland areas is concentrated in complexes of year-round water-retaining ponds. Compared to the Troodos Mountain Range, environmental conditions (i.e. temperature, humidity) within the south-eastern lowlands are significantly different. Namely, the lowland areas are extremely arid

during the day, especially during the summer months (July–September), but retains high humidity (> 70%) and high temperatures (25–30°C) between 18:00–00:00 h and early in the morning (06:00–08:00 h) (Appendix I). Individuals found in the lowland areas differ in their morphology. Namely, individuals in the mountains display three different colouration varieties (morphs; normal, melanistic, and picturata, Fig. 2), while individuals in the south-eastern lowlands display only



Figure 2. The three morphs of Grass Snake encountered on the island of Cyprus, normal (left), picturata (middle) and melanistic (right). Only the normal morph has been recorded at the lowland population of the species. Photos by Marilena Stamatiou.

the normal morph (Baier et al., 2013).

The historical number of population estimates for the lowland (Paralimni and Ayia Napa areas) Grass Snake populations are very limited. Blosat (2002) estimated a population size of between 82–182 individuals (Paralimni only), and Mpakaloudis et al. (2024) estimated between 59–102 individuals (for both the Paralimni and Ayia Napa areas). While these studies are important, they did not take into account the potential crepuscular and nocturnal activity of the species.

Ectotherm species, such as reptiles, have adopted a largely diurnal activity rhythm to effectively thermoregulate (Bogert, 1948; Bertolucci et al., 2002). In some cases, where high daily temperatures and high aridity prevent optimal thermoregulation during midday, individuals may deviate from diurnality following crepuscular and nocturnal activity rhythms (Rutschmann et al., 2023; Perry et al., 2025). More favourable, less intense, environmental conditions after sunset help individuals in their daily activities, including foraging and oviposition (Perry and Fisher, 2006; Amadi et al., 2020; Baxter-Gilbert et al., 2021). With global trends indicating that pressures of climate change will intensify in the following decades, reptile species can either adapt to the new climate conditions, which often include higher air temperatures, or go extinct (Böhm et al., 2016; Biber et al., 2023). For this reason, many diurnal species have started, or are expected to, showcase crepuscular and nocturnal activity (Amadi et al., 2021; Baxter-Gilbert et al., 2021; Levy et al., 2024). The genus *Natrix*, and specifically the Eastern Grass Snake, belongs to the many herpetofauna species that have been reported to be actively engaged in crepuscular and nocturnal activity (Capula et al., 1994; Spaseni et al., 2024).

While crepuscular and nocturnal activity has been documented for *Natrix* spp. (Hailey and Davies, 1987; Mebert et al., 2011; Spaseni et al., 2024), and adaptability of the genus has been widely observed (Luiselli et al., 2005; Weiperth et al., 2014; Andjelković et al., 2016), relevant data for Cyprus is very sparse. Only Blosat (2002) noted that the individuals in the lowlands showcase different daily patterns than their mountain counterparts, being most active during early morning and evening hours. Additionally, Blosat (2005) suggested that they move between ponds during cool nights, making use of the higher humidity conditions and lower ambient temperatures.

Here, we monitored the coastal lowland populations of *N. n. moreotica* in an attempt to estimate its size

and explore the feasibility of a nocturnal monitoring protocol. Our results can contribute to research on reptilian activity patterns in arid island environments, especially under the pressures brought by severe anthropogenic presence and climate change.

Materials and Methods

The study was conducted within the lowland range of the Grass Snake population in Cyprus, at the Paralimni lake (and surrounding areas) and near Ayia Napa (Appendix II). A total of 52 transect lines (100–300 m each) were initially selected using satellite images from Google Earth. All line transects were surveyed in February 2023, and their characteristics (type and condition of the habitat, presence of water, presence of foraging animals, nesting sites, refuge sites, pressures or threats for Grass Snakes) were recorded and validated through field observations. From the 52 transects, the 20 most promising transects considering the assessed presence of the species were selected: 17 transects at the Paralimni lake and three transects at Ayia Napa (Fig. 1). These transects were parallel to bodies of water with known Grass Snake presence or in areas presenting favourable conditions, covering the full known extent of the species distribution at the south-eastern part of the island (Fig. 1, and see Stamatiou, et al., 2026).

The 20 selected transects were repeatedly monitored between March to October 2023. In total, each transect was visited approximately 2.2 times for an average of 40 minutes each (range: 20–90 minutes). During each survey, the team members (MS, GP) would slowly walk the length of the transect line searching for Grass Snakes and then stand still at a vantage point for an additional 15 minutes, looking for Grass Snakes swimming or moving through vegetation. Observations of Grass Snakes were reported using a specific protocol (see Stamatiou, et al., 2026).

Initial surveys (March–July) were conducted during the morning hours (between 06:00–13:00 h) following the standard monitoring procedure. After the end of July, within August–September, following Blosat's (2002) observation, we also conducted night surveys, between 17:00–23:00 h, looking for possible evidence of nocturnal activity.

To estimate population size, we used the Loglinear Models for Capture-Recapture Experiments method, focused on closed population models (Rivest and Levesque, 2001; Borchers and Fewster, 2016). For this, we assumed that the population in the coastal lowland area was “closed” for the period of this study, i.e. no

exchange of individuals, no births or deaths, and no dispersal outside the area. Although observed individuals were not captured, expert opinion in the field, as well as photographic evidence, were used to ensure their identification as different specimens without ambiguity. Recorded data from subadults and adults were analysed using the R package *Rcapture* (Rivest and Baillargeon, 2025) in RStudio (Posit team, 2025).

Results

Throughout the monitoring period (March–October 2023), a total of 30 monitoring visits were undertaken (approx. once a week). A total of 66 transect surveys were conducted, 52 during morning hours (between

06:00–13:00 hrs), and 14 during evening hours (between 17:00–23:00 hrs). The lowest recorded temperature during actively monitoring (regardless of time of day) was 15°C and highest was 28°C (lowest and highest observed in the area during the monitoring months were 5.5°C and 41.5°C, respectively). Snake presence was observed on only four of the 20 transects (Table 1, Fig. 1), accounting for a total of 18 individuals, out of which 13 were observed during evening surveys (Table 2, Fig. 3). From the 18 individuals found, only five were observed in morning hours (0.096 snakes per day effort), while the rest ($n = 13$) were observed during the evening (0.92 snakes per day effort). All observed snakes showcased the normal morph (Fig. 4).

Table 1. Overview of transects with Grass Snake presence, including the specific area (Paralimni or Ayia Napa), transect name, and the number of Grass Snakes observed across all visits for each transect. Additional information on the nature of the water body of the transect, and the present human pressures in the area are given.

Area	Transect Name	Total Visits	Total Snakes Observed	Water Body	Human Pressures
Ayia Napa	AN_1	5	4	Pond, ca. 50*70m	Water pumping
Ayia Napa	AN_2	4	7	Pond, ca. 5*4m	Slight presence of hunters, farmers, tourists
Ayia Napa	AN_3	5	1	Lake, ca. 90*80m	Slight presence of hunters, farmers, tourists
Sotira (Paralimn)	SP_1	11	6	Lake, 40*40 m, plus two canals	Close to residential areas, cultivated fields, cattle, presence of hunters and tourists,

Table 2. Individual Grass Snakes observed. Information is presented on the area (AN = Ayia Napa; SP = Paralimni – Sotira Ponds), the code given to each observed individual, the date, time and temperature of observation, as well as the observed activity.

A/A	Transect	Code	Date	Time	Temp °C	Activity
1	AN_2	M6.2_A	15/06/23	10:00	25	Swimming between riparian vegetation
2	AN_2	M6.2_B	15/06/23	10:00	25	Hidden under branches
3	AN_1	M6.3_A	21/06/23	8:45	24	Swimming between riparian vegetation
4	AN_2	M6.3_B	21/06/23	10:15	28	Hidden under branches
5	AN_2	M7.1_A	04/07/23	9:00	26	Still, undergoing shedding
6	SP_1	M8.1_A	02/08/23	21:00	25	Swimming between riparian vegetation
7	AN_2	M8.3_A	16/08/23	21:00	25	Moving in and out of water, hunting
8	AN_2	M8.3_B	16/08/23	21:30	25	Moving in and out of water, hunting
9	AN_2	M8.3_C	16/08/23	21:30	25	Moving in and out of water, hunting
10	AN_2	M8.3_D	16/08/23	21:30	25	Moving in and out of water, hunting
11	AN_1	M8.3_E	16/08/23	21:00	26	Swimming between riparian vegetation
12	AN_1	M8.3_F	16/08/23	21:00	26	Swimming between riparian vegetation
13	SP_1	M8.4_A	18/08/23	19:00	27	Swimming
14	SP_1	M8.4_B	18/08/23	19:00	27	Swimming
15	SP_1	M8.4_C	18/08/23	20:00	27	Still in canal
16	SP_1	M8.7_A	30/08/23	19:30	26	Swimming
17	SP_1	M8.7_B	30/08/23	20:30	26	Resting in pond bank, then swimming
18	AN_3	M9.2_A	15/09/23	20:00	24	Swimming between riparian vegetation

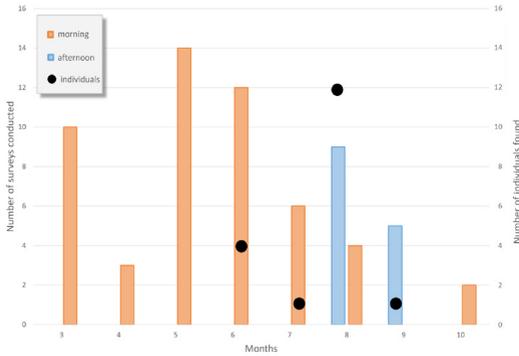


Figure 3. Human effort as the number of monitoring surveys conducted per month (morning or afternoon hours) along with gain, as the number of Grass Snake individuals observed per month.

The four transects where Grass Snakes were observed showcase most of the optimal characteristics to cover the species' ecological needs, alongside lower human pressures (Fig. 5, Appendix II). Out of the four transects, three are situated in the Ayia Napa area, and the other transect is situated at Paralimni, and specifically the Sotira Ponds complex.

When both morning and evening surveys were considered to estimate population size, the Sotira Ponds population was estimated to be between 6–40 individuals (mean = 23), while the population estimate for Ayia Napa was 33–106 (mean = 70), resulting in a total population of the lowland distribution between 39–146 (mean = 93) individuals. When morning and evening surveys were analysed separately, the evening surveys resulted in higher occurrences in both areas (t-test: $p < 0.05$) (Table 3).



Figure 4. Pictures from Grass Snakes observed during the study. (A) An individual undergoing shedding, standing still for hours during morning time, (B) resting between reeds during nighttime, (C) one of the four grass snakes observed foraging at the same pond in the evening, (D) swimming a little before sunset. Photos by Marilena Stamatou (A–C) Giorgos Pishilis GP (D).

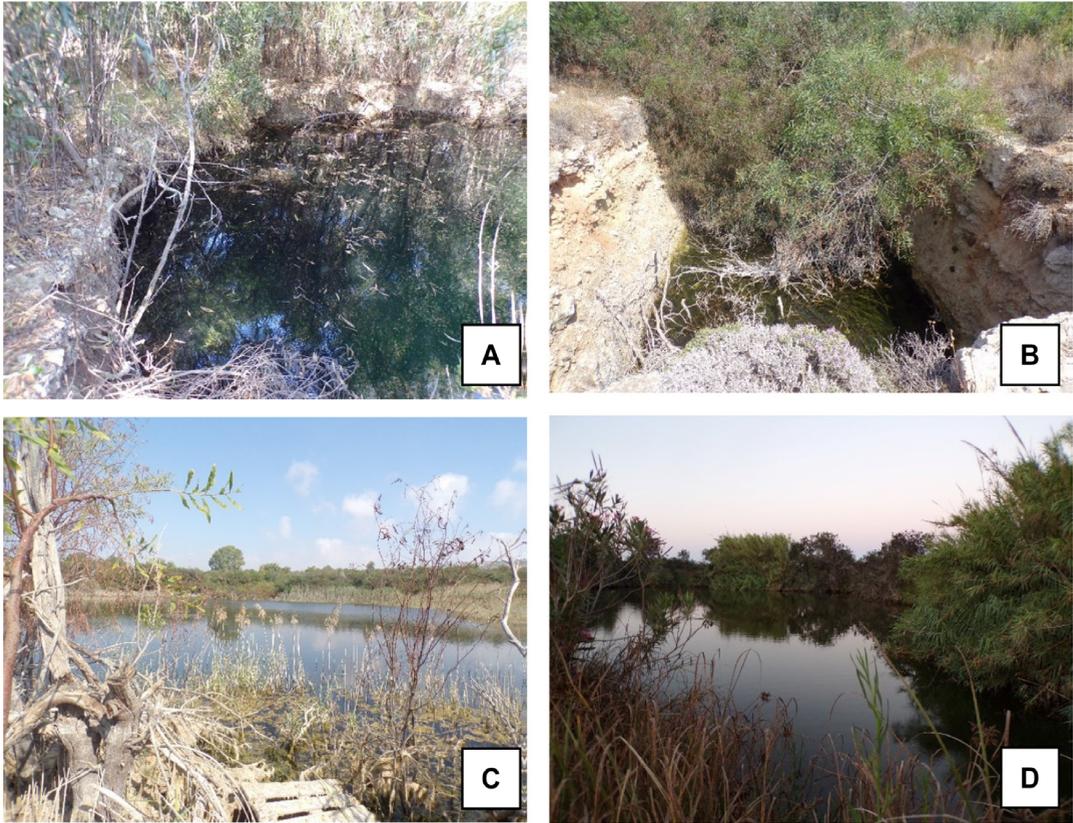


Figure 5. Transects with Grass Snake presence. (A) AN_1, a pond surrounded by thick vegetation, (B) AN_2, a small swallow pond, (C) AN_3, a large open lake surrounded by reeds and (D) SP_1, a large lake with two canals between agricultural land.

Discussion

The genus *Natrix* comprises species inhabiting a variety of different habitats across Europe, with Cyprus hosting one of the southeasternmost populations of the Common Grass Snake, *N. natrix*. Our results show that the studied lowland areas hold a *N. natrix* population ranging between 39–146 individuals (Table 3). The population of each area was calculated at 6–40 individuals for Paralimni, and 33–106 for the Ayia Napa, which differs from the recent work of Mpakaloudis et al. (2024) who used N-mixture models to estimate the presence of between 4–14 individuals for Paralimni lake (Sotira Ponds) and 55–88 for Ayia Napa respectively, adding to a total of 59–102 individuals. The only other historical population size estimate was conducted by Blosat (2002) who used the Lincoln-Petersen-Index to estimate between 82–182 individuals to be present in the Paralimni area, compared to our 6–40 individuals for Paralimni.

While crepuscular and nocturnal activity has long been sporadically reported for the genus from numerous locations (Hailey and Davies, 1986; Mebert et al., 2011; Spaseni et al., 2024), references to it for the Cyprus population are limited to Blosat's work (2002), with

Table 3. Population abundance for the Paralimni and Ayia Napa Grass Snake populations as calculated with R package *Rcapture*. Indicating sample size, and the possible minimum and maximum sizes of the population are noted.

Site	Time	Sample size	Abundance	St.Err.	Min	Max
Paralimni	All	6	23	20.9	6.3	39.7
Paralimni	Morning	0	0	0	0.0	0.0
Paralimni	Afternoon	6	19.3	16.8	5.9	32.7
Ayia Napa	All	12	69.6	64.9	32.9	106.3
Ayia Napa	Morning	5	12.8	10.5	3.6	22.0
Ayia Napa	Afternoon	7	17.6	13.8	7.4	27.8
	All	18	92.6		39.2	146

no further evening surveys conducted for the species in the past two decades, until the present research, taking place in 2023.

Considering our study, the bulk of Grass Snake sightings took place between 19:00–22:00 h (sunset time approximately at 20:00), with fewer records at morning hours. A shortcoming of the present research is that the initial weeks were spent assessing possible areas (most of which did not have recorded populations of Grass Snakes) before starting evening transects. Thus, we strongly consider that the very limited information on the presence of the Grass Snake in Cyprus might not be a product of its own elusiveness, but rather of the methodology followed by scientists until now. Based on our results it appears obvious that during the summer period Grass Snakes on Cyprus adopt a nocturnal activity strategy.

The methodology utilised to monitor a population can directly impact the quantity and quality of results, while it is also constrained by the scientific resources available (Allen and Engeman, 2015; Moussy et al., 2022). Thus, underreporting of population size is – to a degree – an expected shortcoming of many methods, which can be amplified when biases of area, time of day or seasonality are involved (McClure and Rolek, 2023). These biases are often the result of an effort to collect more data by continuously visiting locations with known presence or only conducting field work at times with higher encounter probabilities, instead of the more resource-demanding process of trying to discover new population sites or daily patterns. Such shortcomings become more prominent for species with a limited distribution, low density or presence in areas that are difficult to access (Letting and Monks, 2015; Richardson et al., 2017; Hoefler et al., 2024).

Given the high temperatures and arid conditions in Cyprus, especially in the south-eastern lowlands of the island, following the standard diurnal survey methodology for *Natrix* spp. used in the rest of Europe, was perhaps the wrong choice. Under such conditions, the use of monitoring methods developed for diurnal species might be unsuitable. An adaptation of the survey methodology for Grass Snakes in the lowlands of Cyprus is required to account for crepuscular activity during the hot and arid periods of the year, following monitoring of other snakes with similar shifts in seasonal activity patterns worldwide (DeGregorio et al., 2015; Capula et al., 2016; Rutschmann et al., 2024).

The shift from predominantly diurnal to crepuscular and/or nocturnal activity, for the individuals of Cyprus

lowland population, can be sought in (a) the arid environment and the high temperatures in the area that affects thermoregulation behaviour (Appendix I), (b) the availability of prey during dusk that facilitates foraging, and/or (c) the lack of intense predation and human disturbance during the night. This shift, as supported by our results, indicates that evening surveys to monitor Grass Snakes are more cost-time effective compared to morning surveys considering the days or surveys required per individual observed in areas with a well-known established population.

Amphibian species, which make up most of the Cyprus Grass Snake's diet (Blosat, 2002; Baier and Wiedl, 2013), are more active during evening hours, making crepuscular and nocturnal hunting more efficient and successful for snakes (Mebert et al., 2011). It is noteworthy that a large Whip Snake (*Dolichophis jugularis*) was observed hunting and successfully capturing prey during one evening (20:40 h), pointing to evidence that many (usually diurnal) species have altered their daily patterns to make up for the high daytime temperatures (see Appendix I) and the behaviour of their prey. Evening activity also helps to avoid diurnal predators and human disturbance (Li et al., 2021; Lee et al., 2024). As the Paralimni area is an important wetland for a large number of bird species (EEA, 2019), including herons and egrets that can prey upon Grass Snakes (Mullarney et al., 2007), the activity of Grass Snakes during evening hours can potentially reduce avian predation risk.

Being ectotherms, reptile species are sensitive to changes in temperature and climatic conditions (Taylor et al., 2021). They are amongst the first species to be impacted by global warming and other aspects of climate change (Massot et al., 2012; Paaijmans et al., 2013; Diele-Viegas et al., 2020). Mediterranean regions (including Cyprus), which are already suffering from intense drought periods (Viola et al., 2014; Lionello and Scarascia, 2018; Pérez-Andreu et al., 2018), will be affected intensely, forcing species to either adapt to the new climate conditions, migrate or go extinct (Nunes et al., 2023; Sunny et al., 2023). Ectotherms will be forced to adapt, partly by changing their daily activity patterns, especially when migration options are limited, dangerous, or require the use of very large amounts of energy (Boyle et al., 2016; Inman et al., 2022; Biber et al., 2023). Paralimni lake is surrounded by a dense urban fabric and other barriers (e.g., roads, fences) making dispersal particularly difficult. Taking into account the well-documented plasticity of Grass Snakes, shifts to

crepuscular and/or nocturnal activity might be nothing less than a signal of changing ecosystems, in an effort to try to adapt to the new conditions, both existing and yet to come.

Acknowledgments. This research was conducted through the financial contribution of Societas Europaea Herpetologica, which funded the scientific team through the 2023 SEH Grants in Herpetology 2023 for the project titled “Monitoring the population of the endemic Cyprus grass snake at Paralimni lake”. We also want to thank Athina Strepí and Phidias Gregoriou for their contribution during the field work. Special thanks to Ioannis N. Vogiatzakis for commenting on the early version of this manuscript.

References

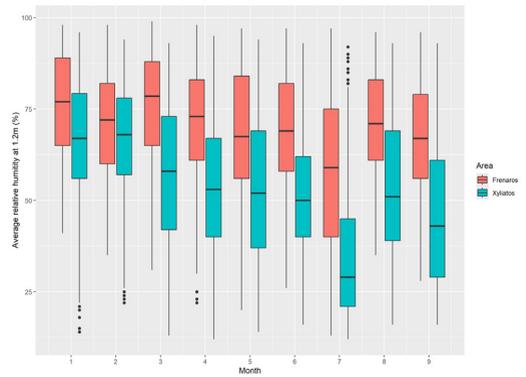
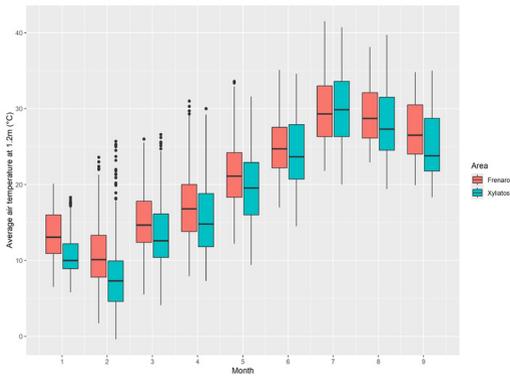
- Allen, L.R., Engeman, R.M. (2014): Evaluating and validating abundance monitoring methods in the absence of populations of known size: review and application to a passive tracking index. *Environmental Science and Pollution Research International* **22**(4): 2907–2915.
- Amadi, N., Luiselli, L., Belema, R., Nyiwale, G.A., Wala, C., Urubia, N., Meek, R. (2021): From diurnal to nocturnal activity: a case study of night-light niche expansion in *Agama agama* lizards. *Ethology Ecology & Evolution* **33**: 515–527.
- Andjelković, M., Tomović, L., Ivanović, A. (2016): Variation in skull size and shape of two snake species (*Natrix natrix* and *Natrix tessellata*). *Zoomorphology* **135**: 243–253.
- Asztalos, M., Ayaz, D., Bayrakci, Y., Afsar, M., Tok, C.V., Kindler, C., Jablonski, D., Fritz, U. (2021): It takes two to tango – Phylogeography, taxonomy and hybridization in grass snakes and dice snakes (Serpentes: Natricidae: *Natrix natrix*, *N. tessellata*). *Vertebrate Zoology* **71**: 813–834.
- Ayres, C. (2012): Scavenging in the genus *Natrix*. *Acta Herpetologica* **7**(1): 171–174.
- Baier, F., Sparrow, D., Wiedl, H.J. (2013): *The Amphibians and Reptiles of Cyprus*. Frankfurt, Germany, Edition Chimaira.
- Baxter-Gilbert, J., Baider, C., Florens, F.B.V., Hawlitschek, O., Mohan, A.V., Mohanty, N.P., et al. (2021): Nocturnal foraging and activity by diurnal lizards: Six species of day geckos (*Phelsuma* spp.) using the night-light niche. *Austral Ecology* **46**: 501–506.
- Bertolucci, C., Foà, A., Tosini, G. (2002): The Circadian Organization of Reptiles In: *Biological Rhythms*, p. 129–143. Kumar, V., Ed., Berlin, Germany, Springer, Berlin Heidelberg.
- Biber, M.F., Voskamp, A., Hof, C. (2023): Potential effects of future climate change on global reptile distributions and diversity. *Global Ecology and Biogeography* **32**: 519–534.
- Blosat, B. (2002): Study for the Conservation and Protection of the Cypriot Grass Snake (*Natrix natrix cyprica*). Field Research and Management Suggestions, Final Report. Nicosia, Cyprus, Department of Fisheries and Marine Research, Ministry of Agriculture, Natural Resources and Environment.
- Blosat, B. (2005): Establishing a captive-breeding program for the endangered Cypriot Grass Snake (*Natrix natrix cyprica*) - Final Report. Nicosia, Cyprus, Department of Fisheries and Marine Research, Ministry of Agriculture, Natural Resources and Environment.
- Bogert, C.M. (1949): Thermoregulation in reptiles, a factor in evolution. *Evolution* **3**: 195–211.
- Böhm, M., Williams, R., Bramhall, H.R., McMillan, K.M., Davidson, A.D., Garcia, A., et al. (2016): Correlates of extinction risk in squamate reptiles: the relative importance of biology, geography, threat and range size. *Global Ecology and Biogeography* **25**: 391–405.
- Boyle, M., Schwanz, L., Hone, J., Georges, A. (2016): Dispersal and climate warming determine range shift in model reptile populations. *Ecological Modelling* **328**: 34–43.
- Capula, M., Rugiero, L., Capizzi, D., Franco, D., Milana, G., Luiselli, L. (2016): Long-term, climate-change-related shifts in feeding frequencies of a Mediterranean snake population. *Ecological Research* **31**: 49–55.
- Cleridou, N., Benas, N., Matsoukas, C., Croke, B., Vardavas, I. (2014): Water resources of Cyprus under changing climatic conditions: Modelling approach, validation and limitations. *Environmental Modelling and Software* **60**: 202–218.
- Conelli, A., Nembrini, M., Mebert, K. (2011): Different Habitat Use of Dice Snakes, *Natrix tessellata*, among Three Populations in Canton Ticino, Switzerland – a Radiotelemetry Study. *Mertensiella* **18**: 100–116.
- DeGregorio, B.A., Westervelt, J.D., Weatherhead, P.J., Sperry, J.H. (2015): Indirect effect of climate change: Shifts in ratsnake behavior alter intensity and timing of avian nest predation. *Ecological Modelling* **312**: 239–246.
- Diele-Viegas, L., Figueroa, R., Vilela, B., Rocha, C. (2020): Are reptiles toast? A worldwide evaluation of Lepidosauria vulnerability to climate change. *Climatic Change* **159**: 581–599.
- EEA (European Environment Agency) (2019): European Nature Information System: Limni Paralimniou. Version 19.4.15. Available at: <https://eunis.eea.europa.eu/sites/CY3000008>. Accessed on 01 February 2026.
- Fritz, U., Schmidler, J. (2020): The Fifth Labour of Heracles: Cleaning the Linnean stable of names for grass snakes (*Natrix astreptophora*, *N. helvetica*, *N. natrix* sensu stricto). *Vertebrate Zoology* **70**: 621–665.
- Giannakopoulos, C., Hadjinicolaou, P., Kostopoulou, E., Varotsos, K.V., Zerefos, C. (2010): Precipitation and temperature regime over Cyprus as a result of global climate change. *Advances in Geosciences* **23**: 17–24.
- Hailey, A., Davies, P.M.C. (1986): Effects of size, sex, temperature and condition on activity metabolism and defence behaviour of the viperine snake, *Natrix maura*. *Journal of Zoology* **208**: 541–558.
- Hailey, A., Davies, P.M.C. (1987): Activity and thermoregulation of the snake *Natrix maura*. *Journal of Zoology* **213**: 71–80.
- Hofer, S., McKnight, D.T., Allen-Ankins, S., Nordberg, E.J., Schwarzkopf, L. (2024): Diverse Methods for Diverse Systems: A Large-Scale Comparison of Reptile Sampling Methods. *Herpetologica* **80**: 40–50.
- Inman, R.D., Esque, T.C., Nussear, K.E. (2023): Dispersal limitations increase vulnerability under climate change for reptiles and amphibians in the southwestern United States. *The Journal of Wildlife Management* **87**: e22317.
- Lee, S.X.T., Amir, Z., Moore, J.H., Gaynor, K.M., Luskin, M.S.

- (2024): Effects of human disturbances on wildlife behaviour and consequences for predator-prey overlap in Southeast Asia. *Nature Communications* **15**: 1521.
- Letting, M., Monks, J.M. (2016): Survey and monitoring methods for New Zealand lizards. *Journal of the Royal Society of New Zealand* **46**: 16–28.
- Levy, K., Wegrzyn, Y., Moaraf, S., Barnea, A., Ayali, A. (2024): When night becomes day: Artificial light at night alters insect behavior under semi-natural conditions. *Science of The Total Environment* **926**: 171905.
- Li, X., Hu, W., Bleisch, W.V., Li, Q., Wang, H., Lu, W., et al. (2022): Functional diversity loss and change in nocturnal behavior of mammals under anthropogenic disturbance. *Conservation Biology* **36**: e13839.
- Lionello, P., Scarascia, L. (2018): The relation between climate change in the Mediterranean region and global warming. *Regional Environmental Change* **18**: 1481–1493.
- Luiselli, L., Filippi, E., Capula, M. (2005): Geographic variation in diet composition of the grass snake (*Natrix natrix*) along the mainland and an island of Italy: the effects of habitat type and interference with potential competitors. *The Herpetological Journal* **15**: 221–230.
- Massot, M., Baron, J.-P., Jean, C., Galliard, J.-F. Le (2012): Ecological Effects of Climate Change on European Reptiles. p. 179–203.
- McClure, C.J.W., Rolek, B.W. (2023): Pitfalls arising from site selection bias in population monitoring defy simple heuristics. *Methods in Ecology and Evolution* **14**: 1489–1499.
- Mebert, K., Trapp, B., Kreiner, G., Billing, H., Speybroeck, J., Henggeler, M. (2011): Nocturnal Activity in *Natrix tessellata*, a Neglected Aspect of its Behavioral Repertoire. *Mertensiella* **18**: 234–236.
- Mertens, D. (1994): Some aspects of thermoregulation and activity in free-ranging grass snakes (*Natrix natrix* L.). *Amphibia-Reptilia* **15**: 322–326.
- Moussy, C., Burfield, I.J., Stephenson, P.J., Newton, A.F.E., Butchart, S.H.M., Sutherland, W.J., et al. (2022): A quantitative global review of species population monitoring. *Conservation Biology* **36**: e13721.
- Mpakaloudis, D., Makridou, K., Saxoni, S., Kotsonas, E. (2024): Final Report: Recording and mapping, conservation measures and conservation objectives for the Cyprus grass snake (*Natrix natrix cypriaca*). Deliverable 4 for the project “Monitoring and data collection for the species *Natrix natrix cypriaca*”. Thessaloniki, Greece, Forestry and Natural Environment Department of Aristotelio University, pp. 76.
- Mullarney, K., Svensson, L., Zetterstrom, D., Grant, P.J. (2015): Guide to the birds of Greece, Cyprus and Europe. Second Edition. Athens, Greece, Hellenic Ornithological Society.
- Nicolaou, H., Lymberakis, P., Pafilis, P. (2014): The reptiles and amphibians of Cyprus. Nicosia, Cyprus, Herpetological Society of Cyprus.
- Paaijmans, K.P., Heinig, R.L., Seliga, R.A., Blanford, J.I., Blanford, S., Murdock, C.C., Thomas, M.B. (2013): Temperature variation makes ectotherms more sensitive to climate change. *Global Change Biology* **19**: 2373–2380.
- Pérez-Andreu, V., Aparicio-Fernández, C., Martínez-Iberón, A., Vivancos, J.-L. (2018): Impact of climate change on heating and cooling energy demand in a residential building in a Mediterranean climate. *Energy* **165**: 63–74.
- Perry, C., Gangloff, E.J., Rutschmann, A. (2006): Warm nocturnal temperatures act as an ecological trap for a diurnal lizard. *Oikos* **205** (7): e11330.
- Perry, G., Fisher, R.N. (2006): Night lights and reptiles: observed and potential effects. In: *Ecological Consequences of Artificial Night Lighting* p. 169–191. Rich, C., Longcore, T., Eds., Washington DC, United States of America, Island Press.
- Richardson, E., Nimmo, D.G., Avitabile, S., Tworkowski, L., Watson, S.J., Welbourne, D., Leonard, S.W.J. (2018): Camera traps and pitfalls: an evaluation of two methods for surveying reptiles in a semi-arid ecosystem. *Wildlife Research* **44**: 637–647.
- Rivest, L.-P., Baillargeon, S., Rivest, M.L.-P. (2019): Package ‘Rcapture’. Version 1.4-4. Available at: <https://cran.r-project.org/web/packages/Rcapture/index.html>. Accessed on 1 February 2026.
- Rutschmann, A., Perry, C., Galliard, J.-F. Le, Dupoué, A., Lourdais, O., Guillon, M., et al. (2024): Ecological responses of squamate reptiles to nocturnal warming. *Biological Reviews* **99**: 598–621.
- Sophocleous, C., Nalbantis, I. (2017): Effect of land use change on flood extent in the inflow stream of lake Paralimni, Cyprus. *European Water* **60**: 147–153.
- Sparrow, D.J., Baier, F. (2016): Reptilia. In: *Wildlife of Cyprus*, p.645–695. Sparrow, D.J., John, E., Eds., Limassol, Cyprus, Terra Cypria.
- Spaseni, P., Sahlean, T.C., Gherghel, I., Zamfirescu, Ş.R., Petreanu, I.C., Melenciu, R., et al. (2024): *Natrix natrix* after dark: citizen science sheds light on the common grass snake’s nightlife. *PeerJ* **12**: e17168.
- Speybroeck, J., Beukema, W., Dufresnes, C., Fritz, U., Jablonski, D., Lymberakis, P., et al. (2020): Species list of the European herpetofauna – 2020 update by the Taxonomic Committee of the Societas Europaea Herpetologica. *Amphibia-Reptilia* **41**: 139–189.
- Stamatiou, M. (2022): Κατανομή του είδους *Natrix natrix cypriaca* στη οροσειρά του Τροόδου [Distribution of *Natrix natrix cypriaca* on the Troodos mountain range]. Unpublished MSc Thesis, Open University of Cyprus, Cyprus.
- Stamatiou, M., Zotos, S., Pishilis, G., Stark, T. (2026): Appendices for publication “Population size and nocturnal activity of Cypriot Grass Snakes, *Natrix natrix moreotica* (Bedriaga, 1882), in an arid island environment”, in *Herpetology Notes*. Available at: <https://doi.org/10.6084/m9.figshare.31376512.v2>. Accessed on 25 February 2026.
- Taylor, E.N., Diele-Viegas, L.M., Gangloff, E.J., Hall, J.M., Halpern, B., Massey, M.D., et al. (2021): The thermal ecology and physiology of reptiles and amphibians: A user’s guide. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology* **335**: 13–44.
- Posit team (2025): RStudio: Integrated Development Environment for R. Available at: <https://posit.co/download/rstudio-desktop/>. Accessed on 1 February 2026.
- Zotos, S., Stamatiou, M., Naziri, A., Meletiou, S., Demosthenous, S., Perikleous, K., et al. (2021): New Evidence on the Distribution of the Highly Endangered *Natrix natrix cypriaca* and Implications for Its Conservation. *Animals* **11**: 1077.
- Zotos, S., Stamatiou, M., Vogiatzakis, I. (2023): The Cyprus Herp

Atlas: An initiative for systematic recording of amphibian and reptile occurrences in Cyprus. Biodiversity Data Journal **11**: e98142.

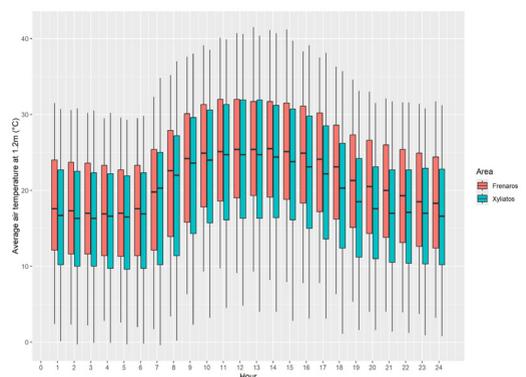
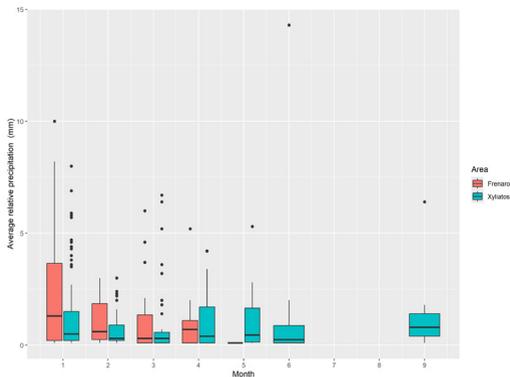
Zotos, S., Stamatiou, M., Vogiatzakis, I.N. (2022): Elusive species distribution modelling: The case of *Natrix natrix cypriaca*. Ecological Informatics **71**: 101758.

Appendix I.



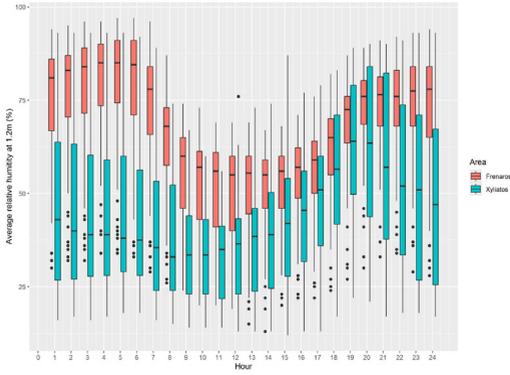
IA. Comparing Average Air Temperature between Frenaros (Close to Paralimni – research site) and Xyliatos (On the Troodos mountain range) areas DATA from The Department of Meteorology – continuously hourly records for the period January – September 2023 (Two-way Anova: $F_{(889,303456)} = 38.39, p < 0.001$).

IB. Comparing Average humidity between Frenaros (Close to Paralimni – research site) and Xyliatos (On the Troodos Mountain range) areas DATA from The Department of Meteorology – continuously hourly records for the period January – September 2023 (Two-way Anova: $F_{(53821,4286293)} = 164.5, p < 0.001$).



IC. Comparing Average precipitation between Frenaros (Close to Paralimni – research site) and Xyliatos (On the Troodos Mountain range) areas DATA from The Department of Meteorology – continuously hourly records for the period January – September 2023 (Two-way Anova: $F_{(46.5,1312.1)} = 14.136, p < 0.001$).

ID. Comparing Average Air Temperature between Frenaros (Close to Paralimni – research site) and Xyliatos (On the Troodos mountain range) areas DATA from The Department of Meteorology – continuously hourly records for the period July – September 2023.



IE. Comparing Average humidity between Frenaros (Close to Paralimni – research site) and Xyliatos (On the Troodos Mountain range) areas DATA from The Department of Meteorology – continuously hourly records for the period July – September 2023.

Appendix II. Locations of the Paralimni and Aya Napa areas and their surroundings that had been visited and assessed at the start of monitoring work to identify habitat suitability for the presence of Grass Snakes ($n = 52$).

