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28.
The Palearctic Watersnakes

28. The Palearctic Watersnakes

Konrad Mebert, Daniel Jablonski

Natrix is a Palearctic genus from northern Africa and temperate Eurasia east to Western China and Pakistan with five semi-aquatic snakes (natricines) currently. They attain a total length of usually around 1 meter, with the larger Grass Snakes rarely growing up to 1.5 meters, and exceptionally longer with the record at 2.05 meters of a specimen from Krk Island, Croatia (Schreiber 1912, cit. in Kabisch 1999). The head is well differentiated from the body, and the tail is rather short. They have large eyes with round pupils. Depending on the species, there are 17 to 23 dorsal scales rows, keeled, less along the paraventral rows. Teeth are aglyphic, and sharp. A Duvernoy's gland is present. The diet consists primarily of amphibians and fish. They are oviparous, with females reaching a larger body size than males. Natricines usually swim on the surface but will submerge when disturbed or hunting for fish and amphibians. They occasionally climb into bushes for thermoregulation, and are usually diurnal but switch to nocturnal activity on warm nights. Predator defense is manifold, individually, and locally variable, and can include in all species tight coiling, head hiding under its body, excretion of musk through bilateral anal glands, triangular flattening of the head and also the body, regurgitating undigested food, death feigning, tail vibration or wiggling, and hissing. The coloration of juveniles and adults are barely different.

Fossil records and current distribution indicate that the genus *Natrix* originated in western Asia (Hecht 1930; Rage and Augé 1993; Ivanov 2001; Guicking et al. 2006b). The genus is monophyletic, a complex with five species, including the Viperine Snake *Natrix maura* Linnaeus 1758, the Dice Snake *N. tessellata* Laurenti, 1768 and the Grass Snake group, a complex of three species with the Eastern Grass Snake *N. natrix* Linnaeus 1758, the Ibero-Maghrebian Grass Snake *N. astreptophora* López-Seoane, 1884, and the Western Grass Snake *N. helvetica* Lacépède, 1789 (Guicking et al. 2006a; Speybroeck et al. 2020). The ancestor of *Natrix* separated in the Miocene and evolved independently into *N. maura* in Northern Africa, and *N. tessellata* in Western Asia. The Grass Snakes (*N. natrix* complex) radiated from ancestral Mediterranean and Caucasus refugia north into Europe and central Asia, also reaching a few islands by marine transgression (Guicking and Joger 2011; Kindler and Fritz 2018; Kindler et al. 2018a; Asztalos et al. 2021b).

Natrix tessellata and the Grass Snake group are sister to *N. maura* that occupies a bas-al position, diverging from the common ancestor about 18–27 MYA. Grass Snakes and *N. tessellata* split about 13–22 MYA. However, newer studies showed more concrete divergence times from a common *Natrix* ancestor to be ca. 21.96 MYA, 18.39 MYA, and 9.58 MYA for *N. maura, N, helvetica*/*natrix*, and *N. tessellata* clades, respectively (Supplementary files in Jablonski et al. 2024a). Intraspecific divergence for *N. maura* begun at approximately 5.3 MYA, for the Grass Snakes (*N. natrix* complex) 6.0 MYA, and for *N. tessellata* 6.7 MYA (Guicking et al. 2006a). In the western Mediterranean Basin, the Messinian Salinity Crisis likely led to the split of *Natrix* species (*maura* and *astreptophora*) between the Iberian Peninsula and Northern Africa, whereas latter *Natrix* populations subsequently split into Moroccan and Algerian-Tunisian clades (Guicking et al. 2008; Kindler et al. 2018a). Even though these semi-aquatic snakes are good swimmers, the 14 km width of the Strait of Gibraltar (passage from the Atlantic into the Mediterranean Sea) was a significant biogeographic barrier for a population exchange (Guicking et al. 2002).

On the previous page. Portrait of a Viperine Snake *Natrix maura*. Photography by Kai Kolodziej.

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Grass Snakes

Konrad Mebert, Daniel Jablonski and Juan M. Pleguezuelos

Eastern Grass Snake
Natrix natrix (Linnaeus, 1758)

Daniel Jablonski and Konrad Mebert

Western Grass Snake
Natrix helvetica (Lacépède, 1789)

Konrad Mebert and Daniel Jablonski

Ibero-Maghrebian Grass Snake
Natrix astreptophora (López-Seoane, 1884)

Juan M. Pleguezuelos and Konrad Mebert

Grass Snakes are among the most common and best-known snakes in Europe and temperate Asia. They are widespread, polytypic and experienced a complex taxonomic history with four (Thorpe 1979) up to 13 subspecies (Kabisch 1999). Fritz and Schmidtler (2020) present a cleaned and updated revision of Grass Snakes taxonomy. Finally, molecular-based studies by Pokrant et al. (2016) and Kindler et al. (2017) on phylogeny and biogeography revealed genetic barriers between three parapatric groups, partly confirming Thorpe's multivariate analysis of quantitative traits of "then" *Natrix natrix* in the 1970s (Thorpe 1973, 1975a, b, 1979), and leading to the recognition of three Grass Snake species: the Eastern Grass Snake *Natrix natrix* (Linnaeus, 1758), the Western Grass Snake *Natrix helvetica* (Lacépède, 1789), and the Ibero-Maghrebian Grass Snake *Natrix astreptophora* (López-Seoane, 1884); described initially as *Coluber natrix* Linnaeus, 1758, *Coluber helveticus* Lacépède, 1789 and *Tropidonotus natrix* var. *astreptophorus* López-Seoane, 1884, respectively.

However, two comprehensive works were composed of detailed information on the Grass Snakes before their recent split into three species: Kabisch (1999) with 67 pages and Blanke et al. (2008) with 312 pages. Therefore, chapters in the following account begin with summary information on the Grass Snakes species as one group, where they exhibit similar traits, but add separated information in subsequent paragraphs where the three species differ from each other, primarily on distribution, morphology, and regional ecology, or present examples of local studies. The order of species treatment roughly follows the chronology of their description and body of information: *natrix, helvetica, astreptophora*.

Distribution and Habitat. The Grass Snake group includes three continents (Hecht 1930; Kabisch 1978, 1999). They occur across most of Europe, north to the limit of the Arctic Circle, and east to central Asia as far as western Mongolia/China. In the south, Grass Snakes occur in northwestern Africa, in the Levant (eastern Mediterranean) historically as far south as Lebanon/Israel, across Türkiye east to the southern shores of the Caspian Sea.

Grass Snakes inhabit a great variety of wetlands, from small streams to large rivers,

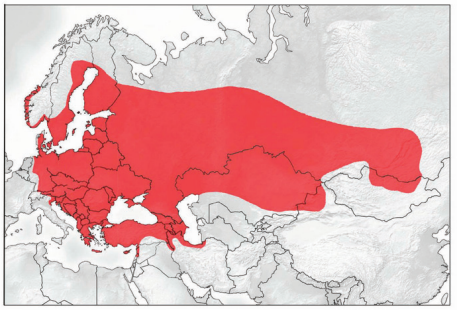

Figure 28.3. The distribution of *Natrix natrix*.

swamps, marshes, and ponds to lakes, where they find their main prey, anurans. But it is also found along coastal habitats and can regionally venture away from water to feed on toads in the humid countryside. Grass Snakes occupy cooler, often shadier, aquatic habitats than the largely sympatric Dice Snake *N. tessellata*, which prefers more open and rockier areas and is primarily a fish predator. The distribution of the single Grass Snake species is as follows:

The Eastern Grass Snake *N. natrix* (type locality: Fada mill pond, Berga-Tuna Estate, Nyköping, Sweden) ranges from northern Europe between Norway, and Finland, with the most northern record from near Gällivare in northern Sweden (Holm 1934 cit. in Kabisch 1999), south to Estonia, Latvia, Lithuania, Poland, Denmark, central (longitude) and eastern Germany, northeastern Switzerland, central eastern Austria, northeastern Italy, Belarus, Ukraine, Czech Republic, Slovakia, Hungary, Romania, Moldova, Slovenia, Croatia, Bosnia and Herzegovina, Serbia, Montenegro, Kosovo, Macedonia, Greece, Albania, Türkiye (Turkey), Russia, Georgia, Armenia, Azerbaijan, Syria, northeastern Iraq, northwestern Iran, southern Kazakhstan, eastern Turkmenistan, northern Uzbekistan, northern Kyrgyzstan, northeast to Aral and Baikal Lakes, northern Mongolia and northwestern China. In the Republic of Georgia, the Eastern Grass Snake inhabits the humid west, where they are observed in ratios of a couple of dozen *N. natrix* to one Dice Snake *N. tessellata*, latter becoming more abundant in drier landscapes (Frotzler et al. 2011). This species also colonized some eastern Mediterranean islands and archipelagos, including Cyclades and Cyprus but not Crete. In central Europe, there is a contact zone with some hybridization between *N. natrix* and *N. helvetica* that runs east along the Rhine River in Germany and northeastern Switzerland, then extends east and through the eastern Alps shared by southeastern Germany, western Austria, and northeastern Italy (Sindaco et al. 2013; Kindler et al. 2017; Schultze et al. 2020; Asztalos et al. 2021a; Milko et al. 2021). Genetic and color pattern characters revealed concordant steep clines across such hybrid zones (Fritz et al. 2023), stabilized by different environmental preferences in one study (Neumann et al. 2024). In Lebanon and Israel, it currently remains unconfirmed and probably is very rare due to anthropogenic habitat changes during 20th Century (see Martens 1996; Grillitsch and Werner 2009). The Eastern Grass Snake is known for elevation as high as 2,289 m in the Armenian Lesser Caucasus (Jablonski et al. 2017) and up to 2,350 m on the Meskheti Range of Georgia (K. Mebert, unpubl. data).

The range of the Western Grass Snake *N. helvetica* (type locality: Jorat, western Switzerland) continues adjacent west to that of the Eastern Grass Snake and stretches from extreme western Germany across France, Netherlands, Belgium, Luxembourg, United Kingdom, and reaching Scotland in the north (Cathrine 2014). In the south it ranges across most of Switzerland, Liechtenstein, western Austria, Italy, and the Mediterranean islands Corsica (France), Sardinia, and Sicily (both Italy). The highest elevation for *Natrix helvetica* is 2,300 m in the Italian Alps (Camerano 1891) and 2,160 m in Ticino, southern Switzerland (authors, unpubl. data). Niche modelling of *N. h. cetti* from Sardinia Island found its habitat to be positively correlated with higher elevation, precipitation, and cooler temperatures (Di Nicola et al. 2023). In the eastern Alps (Austria and Germany), the Western Grass Snake inhabits the mountainous areas. In contrast, the Eastern Grass Snake

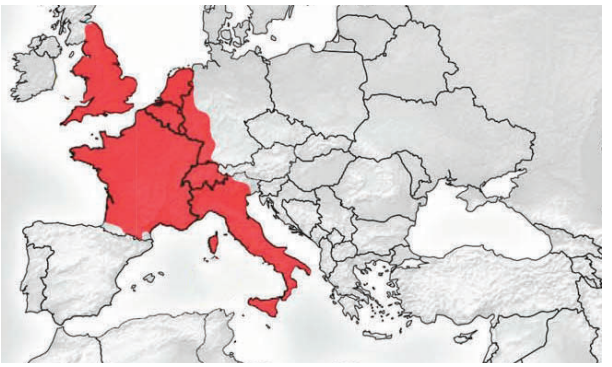

Figure 28.4. The distribution of *Natrix helvetica*.

occupies the lowlands, with some hybridization between them where these two different topographic areas meet (Asztalos et al. 2021a). In far southern France, *N. helvetica* contacts but rarely hybridizes with the Ibero-Maghrebian Grass Snake *N. astreptophora* just north of the Pyrenean Mountains (Pokrant et al. 2016). This hybridization is more frequent in the northeast than in the northwest of the Pyrenean Mountains (Asztalos et al. 2020).

The Ibero-Maghrebian Grass Snake *N. astreptophora* (type locality: La Coruña, Galicia, western Spain) occurs southwest of the Western Grass Snake, from the northern coast of Spain, eastward along the southern slopes of the Pyrenean Mountains to its eastern end where they crossed north into a few departments of southern France. It occupies the following habitats (IUCN Habitats Classification Scheme v. 3.1): temperate forests, temperate grasslands, permanent rivers/streams, bog/marshes/swamps, permanent lakes, seasonal lakes, permanent pools, seasonal pools, springs, alpine wetlands, and sandy shoreline (Pleguezuelos et al. 2010). *Natrix astreptophora* ranges across the entire Iberian Peninsula (Portugal and Spain), between 0–3,200 m a.s.ll and becomes more montane in central and southern Iberia (González-Miras et al. 2008). It is homogenously distributed and abundant in the north, inhabiting the border of beech and mixed forests, dense scrubs, and most river valleys, including those with a high hydrologic seasonality (Santos et al. 2002; Escoriza 2018). To the south, river-associated habitats become more important, but it also dwells in other artificial biotopes, such as humid meadows, ponds, and ditches (Santos et al. 2002; Segura et al. 2007). It is absent from most of the dry Guadalquivir Valley and the arid southeast, where rainfall is below 600 mm (Santos et al. 2002, 2008) and the Balearic Islands (Kindler et al. 2018b). In northwestern Africa, scarce records from northern Morocco, Algeria and Tunisia are mainly restricted to wetlands and humid mountainous forest between 0–2,000 m. Secondarily, it occupies rivers and lagoons close to the Mediterranean coast, where amphibians are numerous, but was occasionally observed also far from water (Schleich et al. 1996; Sindaco et al. 2013; Kalboussi and Achour 2018; Martínez del Mármol et al. 2019). In areas of frequent forest fires in on the western Iberian Peninsula, *N. astreptophora* was only recorded in unburnt plots (Muñoz et al. 2021). On an aridity gradient in the western Mediterranean, the species mainly occupies the more pristine aquatic habitats (Escoriza and Pascual 2021). Mean annual temperature and

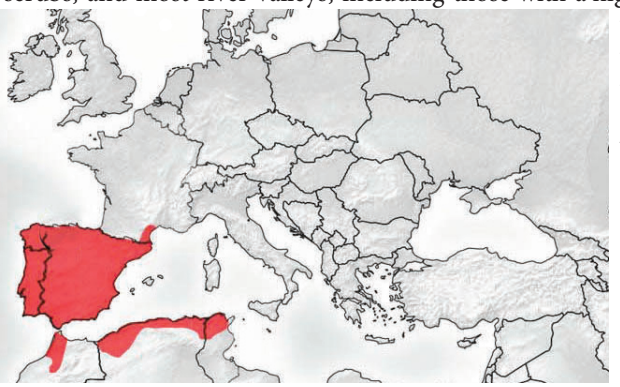

Figure 28.5. The distribution of *Natrix astreptophora*.

precipitation values for northwestern Africa are 16.9ºC and 838 mm, respectively (Escoriza and Ben Hassine 2017). Within southwestern France, it marginally occurs in the departments of Eastern Pyrenees, Aude and Ariege (Geniez 2015; Pokrant et al. 2016; Kindler et al. 2018a; Asztalos et al. 2020; Fritz and Schmidtler 2020).

Identification. The morphological variation of the Grass Snake group led in the past to the description of many subspecies and regional morphs, with the most prominent ones detailed in Kabisch (1978, 1999), that often do not correspond with recently presented molecular phylogenies. It resulted in many misidentifications and unclear distribution patterns. The following accounts summarize morphological characteristics for all three species together, but adds specifics in subsequent paragraphs where each species differs.

Commonly, the Grass Snakes are slender to robust snakes with a total length up to 150 cm, rarely more, with both *Natrix natrix* and *N. helvetica* have been reported of exceptional maximum length > 180 cm (Kabisch 1999), whereas *N. astreptophora* remains smaller with 112.5 cm SVL for a female from the Iberian Peninsula (García-Antón et al. 2017). Females attain larger size with a relatively longer tail in males, e.g., 22.7% of total length for males ver-sus 20.2% for females in southeastern Spain (Feriche et al. 1993). Their dorsal color usually consists of shades of grey, but brown and even reddish tones can also occur (Jablonski et al. 2022). Four rows of dorsal spots or blotches vary in size depending on geographic variation, species, and age. Another traditional name for this group is Ringed Snake, which refers to their white to yellow collar spanning across the neck or being separated into bilateral lunar spots. The collar is orangish in subspecies *N. natrix scutata* of Transcaucasian countries and Russia. On the body and adjacent to the light collar are large, bilateral blotches, often curved and pointed posteriorly. The light collar may disappear in fully grown individuals, whereas the post-collar blotches remain, most frequently in adult *N. astreptophora*. Melanism is widespread and occurs occasionally in single individuals or represents a sizeable proportion in some populations. The iNaturalist dataset showed that the frequency of dark body coloration increases from south to north and west to east (Fritz and Ihlow 2022). The ventral pattern is checkered with black blotches on white ground, with the blotches often exhibiting a concave outer edge (Gonzalez de la Vega 2022). The black proportion of the ventral body increases in size posteriorly to become almost entirely black. Main scale characters (Boulenger 1913; Kreiner 2007; Scali et al. 2011) are dorsal scales keeled and usually arranged in 19 rows mid-body, less prominent keeled to smooth in the lowest (paraventral) two rows; the keeling is also reduced or disappears at the end of the tail. Ventral scales vary geographically but are within 159–189 in males and 155–181 in females, and similarly for subcaudal scales vary within 56–90 in males and 47–74 in females. All three Grass Snake species share the following characteristics: Anal scale is usually divided. Preocular scales: 1, rarely divided. Postocular scales: usually 3, rarely 2 or 4. Upper Labial scales: 7 (rarely 6 or 8); 3rd and 4th touch the eye. Temporal scales: 1 (rarely 2) anterior and 2 (rarely 3) posterior. Roger S. Thorpe has analyzed more detail on geographic variation in multiple studies (see his references from 1973–1989).

In the Eastern Grass Snake *Natrix natrix* northern populations are usually dark greyish, althugh individually in different tones, and with four rows of small dorsal-lateral spots. In southern populations of *N. natrix*, the dorsal pattern contrasts with four rows of larger dorsal blotches, and the lateral ones extended to vertical bars.

Figure 28.6: Natural color pattern variation of Eastern Grass Snakes (*Natrix natrix*) from: A) Poland; B) Slovakia; C) northeastern Türkiye; D) southwestern Türkiye; E) and F) Milos Island, Greece. Photo credit: A), C), D) Konrad Mebert; B) Daniel Jablonski; E) Andre Schmid; F) Laura and Bobby Bok.

Individuals with two light dorsal lines along the body (persa morph) occur in southeastern populations from the Balkans to Türkiye, Caspian Sea, and Syria (subspecies *vulgaris, moreotica*, *scutata*, and possibly *syriaca*). Some distinct color pattern expression on insular populations led to descriptions of different subspecies and morphs (e.g., *N. n. fusca* from Kea Island in Greece, *N. n. gotlandica* from Gotland, Sweden, *N. n. cypriaca* from Cyprus, or *N. n. schweizeri* from the southern Cyclades, for example, Milos Island, Greece), that are invalid from the evolutionary point

of view (Kindler and Fritz 2018). Interestingly, *N. n. cypriaca* and *N. n. schweizeri* have similar body coloration variation: first, the more contrastingly heavily blotched morph on light gray, without or only partly visible light collar band, a second wholly or partly melanistic individual. And third a stippled morph with more minor black and olive-grey flecks, that was named picturata variation (Baier et al. 2009; Zotos et al. 2021). However, current genetic data (Kindler et al. 2013; Asztalos et al. 2021b) support the existence of only four subspecies of *N. natrix* without any insular endemics, even though the southern subspecies, including the polymorphic Aegean populations of *N. n. moreotica*, show generally a higher variability than northern ones (Jablonski et al. 2023c; and see more content below). Thus, these insular phenotypes apparently represent adaptation to local environments in the Mediterranean area. Their scalation characteristics are those of the entire Grass Snake group, however, with a restricted range in the number of ventral and subcaudal scales, 163–188 and 53–89, respectively. The number of ventral scales of males is slightly high-er on average than in females, whereas the number of subcaudal scales is significantly higher in males. The Eastern Grass Snake is slimmer and smaller than western species, with patches behind the head usually richer in yellow to orange, especially in the easternmost populations, ssp. scutata, that is generally missing the lateral vertical bars. *Natrix natrix* females are more robust and reach longer sizes than males. Specimens > 120 cm in total length are uncommon to rare, with the largest specimen found killed on Krk Island, Croatia, and subsequently mea-sured as 205 cm (Schreiber 1912; Kabisch 1999). The weight of adult Eastern Grass Snakes from central Europe ranges on average in males from 100–140 g, in females 300–350 g (Günther and Völkl 1996; Kabisch 1978, 1999).

The Western Grass Snake *Natrix helvetica* dorsal pattern usually consists of two rows of dorsal spots/blotches and vertically elongated lateral bars. The black nuchal blotches are often only little indicated (Kabisch 1999). Specimens of the Italian Grass Snake *N. helvetica sicula* from far southern Italy, e.g., Sicily Island and southern Calabria, are characterized for their orange snout tip and chin. Melanistic specimens are known. The subspecies *N. helvetica cetti* from the islands of Sardinia and Corsica (Vanni and Cimmaruta 2011; di Nicola et al. 2021; Schultze et al. 2020) show a more distinctive morphology: Ventral scales: 158–178 (males 160–178, females 158–173). Subcaudal scales: 47–64 pairs (males 56–64, females 47–53). Preocular scales 1, but often 2 at least on one side of the head. Adult Western Grass Snake sometimes lack the typical light collar band.

An external character of *Natrix* astreptophora relates to its epithet "*astreptophora*" (López-Seoane 1884: p. 15) that denotes the absence of the white to the yellowish collar in adults, which is still present in juveniles (Braña 1998; Fritz and Schmidtler 2020). Besides the black blotches posterior to the light collar standard in most Grass Snakes, some juvenile *N. astreptophora* also show an additional distinctive black parietal band anterior to the light collar band (Pleguezuelos 2018). Most specimens show a reddish iris, the most visible external diagnostic character to distinguish against the parapatric *N. helvetica* (Pokrant et al. 2016), but also exhibit a black patch crossing diagonal over the lower anterior portion of the iris that also occurs in some southern *N. natrix* and *N. helvetica* (Gonzalez de la Vega 2022). Newborn body color is brown to olive or ocher after the first ecdysis, whereas adults are grey with the occasional reddish-brown morph (Gonzalez de la Vega 2022). On the dorsum, 3–6 longitudinal rows of 41–56 black spots often disappear in adults (pattern less), and rarely fuse across the back, as in other Grass Snakes (Geniez 2015). Up to 5.4% of individuals in Cantabrian Mountain populations are melanistic (Meijide and Pérez-Melero 1994; Albadalejo 2008). The Ibero-Maghrebian Grass Snake has a wide head and stout muscular body, showing differences in skull bones from the other Grass Snakes (Pokrant et al. 2016).

Phylogeny and phylogeography. The extant diversity within Grass Snakes (Deepak et al. 2022) suggests that the group originated in Asia, afterward dispersing to the western Palearctic, where they diversified into the current species of the genus (Schöneberg et al. 2023). First comprehensive morphological studies on Grass Snakes by Thorpe (e.g., 1973, 1975a, b, 1984, 1979) were followed by molecular studies (Guicking et al. 2006; Fritz et al. 2012; Kindler et al. 2013). They evaluated phylogeographic structure and time of divergences with subsequent studies of hybrid zones, morphology, and osteology (Pokrant et al. 2016; Kindler and Fritz 2018; Kindler et al. 2017, 2018a,b; Schultze et al. 2020; Asztalos et al. 2020, 2021a, b), finally resulting in significant changes in the taxonomy and phylogeny of the traditional Grass Snake *Natrix natrix*, by recognizing three well-separated parapatric species. The Ibero-Maghrebian Grass Snake *N. astreptophora* was the first to diverge from other Grass Snakes in Europe at 9.6–10.6 MYA, resulting from the uplift of the Pyrenean Mountains (Pokrant et al. 2016). This was reanalyzed and adjusted to a slightly younger split by Schöneberg et al. (2023), see below. Subsequently, the Grass Snakes in Europe split into the Eastern Grass Snake *N. natrix* and the Western Grass Snake *N. helvetica* approximately 8.2 to 7.3 MYA (Fritz et al. 2012; Kindler and Fritz 2018; Kindler et al. 2017). The Big-head Grass Snake *N. "megalocephala"* (Orlov and Tuniyev, 1987) from the Caucasian region and northeastern part of the Black Sea coast was often listed as a separate species. However, a molecular-phylogenetic analysis revealed it only as a variation, possibly an ecomorph or ecophenotype of *N. natrix*, that occurs widespread as far as Switzerland (Göçmen et al. 2011a) and was ultimately synonymized with this species (Kindler et al. 2013; Asztalos et al. 2021a).

The Eastern Grass Snake *N. natrix* continued diversification around 6 MYA (Kindler et al. 2017) with the following, currently recognized subspecies (Kindler and Fritz 2018; Fritz and Schmidtler 2020; Asztalos et al. 2021a, b): *N. n. natrix* (Linnaeus, 1758); *N. n. vulgaris* (Laurenti, 1768); *N. n. moreotica* (Bedriaga, 1882), *N. n. scutata* (Pallas, 1771), with one potential subspecies, *N. n. syriaca* (Hecht, 1930), that requires more attention. Recent data based on mitochondrial and nuclear DNA show, *N. n. natrix* occurs in Sweden, Norway, Finnland, Denmark, and Germany, except its western part. It forms possible broad contact zones with the subspecies *N. n. vulgaris* in Poland, Czech Republic, and Slovakia. This subspecies probably is widespread in southern Central Europe, northeastern Italy as far south as Argenta and Ravenna, and large parts of central Balkan countries. It is replaced in western and southern Balkan and Western Türkiye by *N. n. moreotica.* The areas farther east, from the Baltic republics through Ukraine, the Middle East and Iran to Mongolia is inhabited by the subspecies *N. n. scutata* (Asztalos et al. 2021a, b; Jablonski et al. 2023a)

Diversification in the Western Grass Snake *N. helvetica* began after establishing the old-est lineage for in the most southern (Italian) populations with an estimated mean age of 6.8 MYA. Currently, three or four subspecies are recognized: first, *N. h. helvetica* of western Europe, and second *N. h. sicula* (Cuvier, 1829) of Italy that includes now also *N. h. lanzai* (Kramer, 1970). The Tyrrhenian Grass Snakes from the Italian island of Sardinia, *N. h. cetti* (Gené, 1839), and the neighboring French island of Corsica, *N. h. corsa* (Hecht, 1930), represent the third and fourth subspecies, or they become synonymized with each other, pending further investigation (Fritz et al. 2012; Kindler and Fritz 2018; Fritz and Schmidtler 2020; Schultze et al. 2020). The nominotypic *Natrix h. helvetica* also occurs across most of Switzerland and France, and to northern Netherland including Belgium and Luxembourg (van Riemsdijk et al. 2020; Ahnelt et al. 2021) and Great Britain, barely reaching into Scotland (Cathrine 2014); southwards it reaches the Spanish Valle de Arán in the northern slope of the Pyrenean Mountains. It introgresses in northwestern Italy into *N. helvetica sicula*, the Italian Grass Snake, that primarily inhabits mainland Italy and Sicily

Island, but also southern Switzerland and across the Alps of Western Austria into far southern Bavaria, Germany (Schultze et al. 2020; Asztalos et al. 2021a, b).

The Ibero-Maghrebian Grass Snake *N. astreptophora* is the sister taxon to *N. helvetica*. These two Grass Snakes species from western Europe and northweastern Africa form the sister clade to the older group of Eastern Grass Snake *N. natrix* (Schöneberg et al. 2023). *Natrix astreptophora* split from the Western Grass Snake *N. helvetica* in the upper Miocene (7.3 MYA, confidence interval 5.86–10.59 MYA; Schöneberg et al. 2023). There is also morphological and molecular evidence for some hybridization between *N. astreptophora* and *N. maura* (Gonzalez de la Vega 2022; Schöneberg et al. 2023). *Natrix astreptophora* is genetically structured into three clades. First, the European (Portugal and Spain) and northwest African *N. astreptophora* diverged 5.44 MYA from each other (Kindler et al. 2018a). Second, the North African Grass Snakes split again into two groups on both sides of the Mouluya Valley, forming the Moroccan and Tunisian/Algerian clades. Both previous splits likely occured as a result of the Zanclean flooding event of the dried Mediterranean Basin at the end of the Messinian Salinity Crisis (Kindler et al. 2018a). Latter group was subsequently re-established as *N. astreptophora algerica* (Hecht, 1930) by Fritz and Schmidtler (2020). On the northern side of the Pyrenean Mountains in southeastern France, *N. astreptophora* and *N. helvetica* are parapatric, with a steep genetic transition between them, and rare hybridization (Pokrant et al. 2016; Asztalos et al. 2020). This contact zone had established after the mid-Holocene range expansion from glacial refuges on the Iberian Peninsula (*N. astreptophora*) and southwestern France (*N. helvetica*).

Population Aspects. Newborns of all three *Natrix* species exhibit a total length of 14–22 cm (usually 18–19 cm) and weigh around 2–4 g (Kabisch 1999). Before their first hibernation, they reach a total length of 25–30 cm, to 50–60 cm at five years, to 70 cm at 7–8 years, and to > 100 cm at 15 years of age; usually only females' growth larger than 80 cm of total length, some of them reaching 17–18 years of age (Madsen 1983; Braña 1998). Females grow faster than males but require more time to mature and generally attain greater length and weight. In *N. natrix*, males reach sexual maturity at about 50 cm total length and 50 g weight at the age of three years, whereas males of *N. astreptophora* in southeastern Spain, mature at 30 cm snout-vent length (SVL; approximately 40 cm total length). Females of all Grass Snake species reach sexual maturity in the fourth or fifth year of life, at approximately 60 cm SVL and 80 g in weight (Jusczyk 1974; Madsen 1983; Rehák 1992; Feriche 1998). In northern Morocco a male at 38.7 cm snout-vent length and a female at 67.8 cm snout-vent length were adults (Fahd 2001). After the age of 8–9 years, growth slows down and may become negligible (Madsen 1983). However, locally reduced food availability can result in females growing slower and to a smaller size; for example, an insular population in Sweden that feeds exclusively on generally smaller newts (the only available amphibians) than females from the mainland that were feed-ing on larger anurans (Madsen and Shine 1993). The sex ratio of *N. natrix* for males:females from northern populations ranges from 1:1.36 to 1:1.5, respectively (Rehák 1992, refs. in Kabisch 1999), whereas those from Iran were 1:1 (Ahmadzadeh et al. 2011), for *N. astreptophora* 1:1.9 in northern Spain (Braña 1998) and 1:1.4 in southeastern Spain (Feriche 1998).

Grass Snakes can be very common in suitable habitats with about 1–7 individuals/ha and reach high densities of close to one individual per square meter during aggregation for mating and feeding when mates and prey temporarily occur at high densities (Tuner 1977; Mertens 1995; Kabisch 1999 and refs.; Sidorovich et al. 2008). The mean total home range for individ-uals in Sweden and Germany were 21.2 ha and 16.4 ha, respectively, and the adjusted home range that excludes large areas never used by the snakes showed a mean of 11.8 ha and 15.1 ha, respectively (Madsen 1984; Mertens 2008), and increased to 39.7 ha in

agricultural impacted area, where seasonally required sites were more distant to each other (Wisler et al. 2008). Indeed, seasonally varying locations have been found for different annual activities, including hibernation, mating, oviposition, and foraging in *N. natrix* in Germany and *N. helvetica* in the Netherlands, with migratory distances of up to 7 km between seasonal sites (Janssen and Völkl 2008). Maximum age by mark-recapture methods was given as 28 years from a Swedish population (Edelstam 1989).

Activity and Thermal Biology. In Central Europe, the Eastern Grass Snake starts emerging from hibernation (rodent burrows, rock crevices, cellars, composts, piles of leaves, subterranean tree roots) in late March or early April and remains active until late September to early October. In southern France, they emerge from hibernation usually on day 95 (Julian calendar; Prodon et al. 2020). Exceptionally, this species can also be found in November or in February, for example, during short spells of warmer temperatures, or probably is more active throughout the year in warmer regions of southwestern Asia, e.g., Azerbaijan (Rehák 1992, D. Jablonski, unpubl. data). In spring and autumn, activity peaks in the warmest hours of the day, usually mid-day into the afternoon, whereas the summer activity has two peaks, in the morning between 0630 h and 0800 h, and late afternoon/evening, respectively (Mertens 2008). During hot days, foraging is conducted at nights (Spaseni et al. 2024). However, nocturnal foraging can be added in cooler spring nights, during high amphibian breeding activity (e.g., Albania, Northern Macedonia, Switzerland, Germany, Mertens 1994, 2008, authors pers. obs.). Referenced accounts in Kabisch (1978, 1999) show that *N. natrix* (and likewise *N. helvetica*) experience a wide range of environmental temperatures during daytime activity, as low as 6° C and > 30° C, but usually somewhat between 18–25° C (Gregor 1980; Kühnel 1993), with preferred body (cloaca) temperatures ranging from 29–33° C (Mertens 1994, 2008). Severe cold weather during the winter months is survived in hibernacula, sometimes with other reptiles such as the Northern Viper (*Vipera berus*), Smooth Snake (*Coronella austriaca*), or the legless lizard Slow Worm (*Anguis fragilis*). Mertens (2008) radiotelemetry hibernating Grass Snakes in complex rodent burrows and found their subterranean position constantly at 5–15 cm depth, and only during a freezing period with temperatures less than –10° C snakes move into lower layers, between 25–50 cm depth.

Often, the visibly highest activity relates to the mating period in the spring months when males search for females. For example, in a mosaic landscape of woods, pastures, agricultural fields and ponds in Sweden, Madsen (1984) observed an average movement of 54.8 m per day by Grass Snakes, whereas later in the summer, they remained more sedentary (average movement per day 13 m). However, neither a higher movement of male Grass Snakes nor a reduced summer activity was found in a similar study and habitat in central Germany (Mertens 2008). Instead, larger individuals followed large toads that had left the ponds/pools into more lightly forested sections, whereas smaller individuals remained in the ponds to forage on water frogs. Yet only 4.8% of telemetered individuals were detected in water (Mertens 2008).

The Western Grass Snake *N. helvetica* yields a comparable variation of activities and thermal biology as its eastern sister species (see accounts in Kabisch 1999). For example, in western Switzerland, female *N. helvetica* used monocultures managed by a cropping system, e.g., wheat, potato, and corn (Wisler et al. 2008). The monocultures provided suitable basking sites, favorable foraging grounds, and low pressure from avian predators. Adjacent edge hab-itat (dam, canal bank, forest edge) was preferred for the period of shedding and oviposition. After oviposition, the females returned to the monocultures to hunt amphibians primarily. The mean home range size was 34 ha (Wisler et al. 2008). While the latter study found no nocturnal behavior, night foraging was observed in Western Grass Snake occupying warmer regions, e.g., by the predominantly nocturnal Sardinian subspecies *N. helvetica cetti* (Capula et al. 1994).

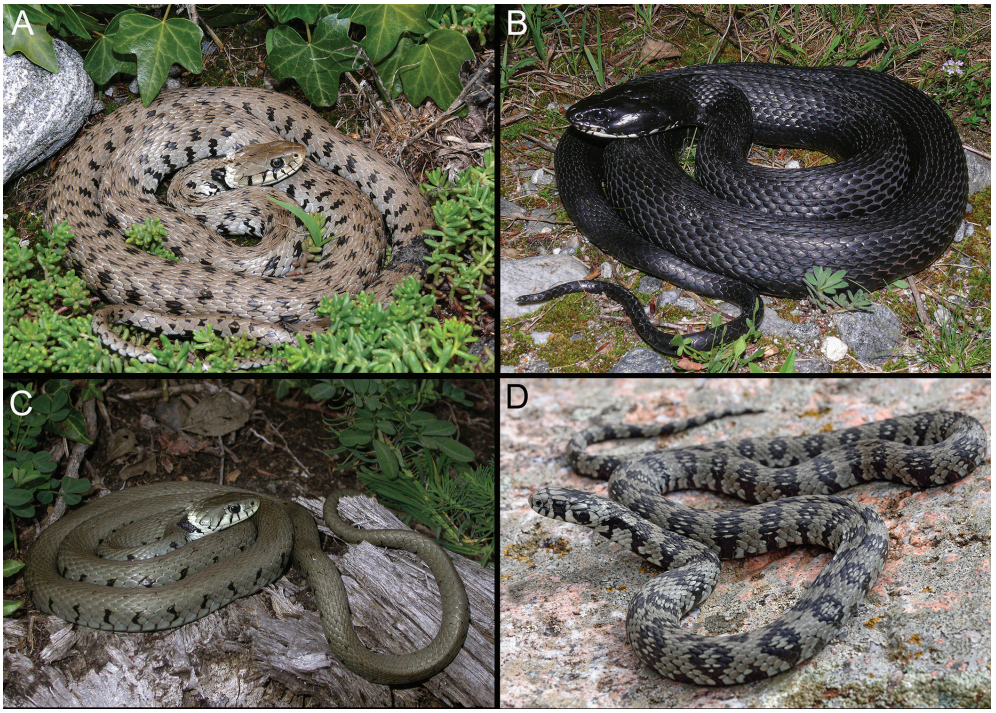

Figure 28.7: Natural color pattern variation of Western or Barred Grass Snakes (*Natrix helvetica*) from: A) and B) Ticino, southern Switzerland; C) western Switzerland; D) Sardinia Island, Italy. Photo credit: A), B), C) Konrad Mebert; D) Matteo Riccardo di Nicola.

The activity season of the Ibero-Maghrebian Grass Snake *N. astreptophora* ranges between March and October in southeastern Spain (Feriche 1998) and between the end of February and early November in the western part of the Iberian Peninsula (Galán and Fernández-Arias 1993; Malkmus 1997), with most records from April to September (Galán 1988). In northern Morocco, active individuals have been found between May and October (Fahd 2001), whereas in Tunisia, *N. astreptophora algerica* is also active during mild winter days (Kalboussi and Achour 2018). Communal hibernation dens with up to three individuals have been detected in Galicia (Galán and Fernández-Arias, 1993). In southeastern Spain, the mean annual body temperature of active individuals was 26.6° C (range 22–32° C), higher during summer with 27.8° C (24.3–32.0° C), less with 26.8° C (19.0–30.0° C) during spring and autumn (Hailey and Davies 1986a; Hailey et al. 1982).

Reproduction. All three species of Grass Snakes appear to have a similar reproductive base strategy, which likely has been adapted to local environmental conditions rather than species constraints. The mating period for Grass Snakes begins soon after emergence from hibernation, in March/April, and can last into May/June, followed by oviposition between June and August (Feriche 1998; Kabisch 1999; our pers. obs.). Males begin courtship primarily after first shedding, raise their head next to a receptive female, twitch their bodies while tongue flicking, followed by pressing their bodies against the female, wrapping their tail around hers, and finally inserting one, rarely both, hemipenis into the female´s cloaca. Copulation takes several minutes, sometimes hours (Rehák 1992). There are mating aggregations with up to 50 snakes (Berec et al. 2015), while some engage in a mating ball, consisting of one receptive female with up to 20 males entangling her (Kabisch

1999). Larger males are more successful in this case, even though no direct fights for females have been observed (Luiselli 1996).

Mating in autumn (September/October) occasionally occurs in Germany, with egg clutches discovered in November/December (Kabisch 1999 and refs. therein). Spermatogenesis in males persists until the end of the mating season. After mating, sperm remains in the female's body, and fertilization is delayed until the onset of ovulation next spring (Berec et al. 2015). In northern Iran (*N. natrix*) and Spain (*N. astreptophora*), females start vitellogenesis in May/early June, with the growth of ovaries continuing at least until mid-July to August (Galán and Fernández-Arias 1993; Feriche 1998; Ahmadzadeh et al. 2011; Shiravi et al. 2012). In cool and rainy Asturias, northern Spain, there are female *N. astreptophora* with oviductal eggs during July and embryogenesis in the early stages at oviposition (Braña 1998). Males from Iran (*N. natrix*) and Spain (*N. astreptophora*) showed signs of a postnuptial spermatogenesis with slow and constant growth in late spring, reaching its height in August and September, ending in November, with sperms stored over the winter for the next spring mating (Faghiri et al. 2011; Arragayago and Bea 1988). Sperm storage may last long, exemplified by a solitary kept Grass Snake that produced fertilized eggs after > 2 years (Hediger 1971; cit. in Eckstein 1993).

Oviposition ranges from June to August, with clutch size from 8–32 eggs per female (Kabisch 1999). Clutch size can geographically range, for example, for *N. astreptophora*: 9-26 eggs in Asturias, northern Spain (Braña 1998), 12-29 eggs in southeastern Spain (Feriche 1998), 6-50 eggs in Galicia (Galán and Fernández-Arias 1993), 10-50 eggs in all of Morocco (Bons 1967), and 11–28 eggs only in northern Morocco (Fahd 2001). Clutch size is also positively correlated with female body size and age for all Grass Snake species (Madsen 1983; Rehák 1992; Feriche 1998). For example, petite females from a food-depauperated habitat on Gotland Island, Sweden, laid only 2–3 eggs (Edelstam 1989), whereas huge females exceptionally deposited around 70–100 eggs (Kabisch 1999 and refs. therein). The size of the egg ranges from 21–40 x 11–24 mm, and the eggs increase in weight by ca. 30% during the incubation (Kabisch 1999). Clutches are deposited in manure piles, sawdust, and rotting vegetables under rocks and rodent burrows. Several females might lay clutches in one suitable place, sometimes with other species, e.g., *Natrix maura* or Aesculapian Snake *Zamenis longissimus*. Communal nests have been recorded in different countries, e.g., 400 hatchling Grass Snakes emerged from one nest in Galicia, Spain (Galán and Fernández-Arias 1993), 558 eggs in the Czech Republic (Berec et al. 2015), and even between 3000–4000 eggs in a pile of sawdust in eastern Germany (Kabisch 1999). Depending on their geographical location, the young hatch from July to September after an incubation period of approximately two months.

Foraging and Diet. Grass Snakes are diurnal, terrestrial, and visually guided active hunters (Hailey et al. 1982; Hailey and Davies 1986a, b), that hold on to their slippery prey until the ingestion process begins (Galán and Fernández-Arias 1993). However, they switch to crepuscular and nocturnal foraging during summer or in generally warmer regions in the south (e.g., Hailey and Davies 1986a; Schleich et al. 1996, pers. obs.). For example, Ibero-Maghrebian Grass Snakes, *N. astreptophora* from Galicia, Spain, avoided activity during the hot midday hours in captivity but under natural light and temperature conditions (Galán 1988). There are also a few reports of marine observation, some for foraging, e.g., a Grass Snake that became entangled in a fishing net at 8–9 m depth in Norway, whereas others might be drifted away by sea currents, one up to 47 km (Kabisch 1999 and refs.). Small prey can be swallowed underwater, while larger prey is carried and then swallowed on land (Schleich et al. 1996). One prey, the Natterjack Toad *Epidalea calamita*, avoids shelter containing the scent of *N. astreptophora* (Gonzalo et al. 2008).

Studies have revealed a broad diet for Grass Snakes, yet always with a focus on common amphibians, primarily frogs of the genus *Rana* and *Pelophylax*, and toads of the genus *Bufo*, rarely the genus *Pelobates* (Kabisch 1999). In contrast, other prey types are less frequently consumed, e.g., poisonous amphibians such as the Fire-bellied toads *Bombina* spp., salamanders and newts, lizards, invertebrates, birds, eggs, and mammals (Rehák 1992; Luiselli et al. 1997; Scali et al. 2011; di Nicola and Bruni 2020). Grass snakes consume a lot of available food at once and can fast for a long time, reportedly until about one year (Dobreff 1939). During the metamorphosis of *B. bufo* tadpoles, *N. natrix* can eat many juvenile toads (Berec et al. 2015). For more information on the diet across all three grass snake species, see also: Luiselli and Rugiero (1991); Gled-Owen (1994); Filippi et al. (1996); Reading and Davies (1996); Luiselli et al. (2005); Faraone et al. (2010); and a particularly extensive account given in Kabisch (1999).

Some specific diet studies on the Eastern Grass Snake *N. natrix* show the proportion of fish consumed: 4.1% of the catch in Bulgaria (Beshkov and Dushkov 1981), 40.8% in Croatia with the remainder being amphibians (Janev Hutinec and Mebert 2011), whereas a Swedish populations fed mainly on fish from the seashores (Andrén and Nilson 1981). In an alpine population of *N. natrix* in northeastern Friuli Venezia Giulia, Italy, anurans were the most frequent diet (*Bufo bufo* 46%, *Rana temporaria* 40%), followed by urodeles (*Salamandra atra* 6%, *Ichthyosaura alpestris* 5%), but also a few lizards (*Zootoca vivipara*) and mice (*Apodemus sylvaticus*) were consumed (Luiselli et al. 1997).

In southeastern England, the diet of small and medium-sized of the Western Grass Snake *N. helvetica* is mainly based on aquatic prey with a predominance of anurans (63%, primarily introduced *Pelophylax* spp.), fish (25%) and rarely a bird (1%). Grass snake usually swallowed prey headfirst (65%), however, this depended on the prey type (Gregory and Isaac 2004). The principal prey of *N. helvetica* on the Italian mainland consisted primarily of the toad species *Bufo bufo* and the frog genus *Rana*, and rarely included rodents, fish, saurians, invertebrates and passerine (Scali et al. 2011; Di Nicola & Bruni, 2020). The main prey of Sardinia´s *N. helvetica cetti* were the frogs *Discoglossus sardus* and *Hyla sarda*, and rarely lizards such as *Podarcis tiliguerta* (Scali et al. 2011). Amphibian larvae, including those of newts, are food mainly for juveniles.

Data from Galicia, Asturias, and Levante for the Ibero-Maghrebian Grass Snake *N. astreptophora*, show the major prey are amphibians. Species include *Discoglossus galganoi, Bufo spinosus, Alytes obstetricans*, and the urodele *Salamandra salamandra* and less often oligochaetes, insects and microtines (Braña 1998; Pleguezuelos 2018). Furthermore, prey species recorded for *N. astreptophora* are anurans (*Epidalea calamita, Pelophylax perezi, Rana temporaria, R. parvipalmata, R. iberica*), urodeles (*Lissotriton boscai, L. helveticus, Triturus marmoratus, T. alpestris*) and amphibian larvae, fishes (*Leuciscus* sp., *Phoximus* sp.), other vertebrates (*Riparia riparia*), and insects (Garzón 1974; Valverde 1974; Vericad and Escarré 1976; Galán 1988; Meijide 1989; Galán and Fernández-Arias 1993; Braña 1998; Díaz 2004; Galán and Ferreiro 2010; Ayres 2012; S. Busack per. com.). Frequency of amphibian prey is between 80–98%, but certainly will vary by season and location. In Morocco, the anurans *Discoglossus scovazzi, Pelophylax saharicus,* and the lizard *Chalcides* sp. have been recorded as prey (Bons 1967). In Tunisia, *N. astreptophora* is a predator of *Bufo spinosus* (Ben Hassine and Escoriza 2014).

Predators and Defense. The Eastern Grass Snake *N. natrix* faces a broad spectrum of vertebrate predators, from fish to reptiles, and carnivorous mammals including domestic cats, but primarily from dozens of bird species (Kabisch 1999). Young Grass Snakes are frequently preyed on even by invertebrates such as the Golden Ground Beetle (*Carabus auratus*), but also by anurans, passerines, chickens, hedgehogs, moles, and mice (Kabisch

1999). For all Grass Snakes, the Short-toed Snake Eagle (*Circaetus gallicus*) has a particular reputation as a formidable snake hunter (Pleguezuelos 2018; Pleguezuelos and Ontiveros 2010). According to Zebe (1936, cit. in Kabisch 1999), an adult pair of Short-toed Snake Eagle and their single young may consume up to 1000 snakes per season, although when preying on larger colubrids compared to smaller vipers, the figure of 450 snakes per eagle family and season, is more credible (our unpub. data). Near Minsk, Belarus, Short-toed Snake Eagles largely prey on *N. natrix* (Glutz von Blotzheim et al. 1971).

Likewise for the Western Grass Snake *N. helvetica,* e.g. from Loir-et-Cher, France, where the Short-toed Snake Eagle only fed on that species and the Asp Viper *Vipera aspis* (Perthuis 2008), apparently feeding on the locally most frequent and sizable snake species (Maumary et al. 2013). However, in the Montados, southern Portugal, snake eagles rarely fed on grass snakes (Onofre and Sampaio 2020). Furthermore, all Grass Snakes are preyed by herons, egrets, storks, owls, kites, falcons, Egyptian Vulture, otters, felines, martens, crabs, and also by other snakes. In particular the Western Montpellier Snake *Malpolon monspessulanus* preys on *N. helvetica* and *N. astreptophora*, whereas the Eastern Montpelier Snake *M. insignitus* preys on *N. natrix* (Díaz-Paniagua 1976; Schleich et al. 1996; Vacher and Geniez 2010; Pleguezuelos 2018; Jablonski et al. 2024b).

The Eastern Grass Snake *N. natrix* is infected by many parasites. From Iran, Yossefi et al. (2014) reported *Rhabdias fuscovenosa* (Nematoda), *Telorchis assula* (Digenea), and *Ophiotaenia europaea* (Cestoda). In Türkiye *N. natrix* was infected by five species of Digenea: *Astiotrema monticelli*, *Encyclometra colubrimurorum*, *Macrodera longicollis*, *Paralepoderma cloacicola*, and *Telorchis assula*; two species of Cestoda: *Ophiotaenia europaea* and *Spirometra erinaceieuropae*; and two species of Nematoda: *Rhabdias fuscovenosa* and larvae of *Eustrongylides excisus* (Yildirimhan et al. 2007, and refs. therein for other countries). Lewin (1992) reported 21 types of parasites from Poland, including six adult trematodes, five meso- and metacercariae, one cestode larva, five adult nematodes, two nematode larvae, one acanthocephalan and one tick. A more recent review from Poland revealed > 25 species of parasites for *N. natrix* (Kuśmierek et al. 2020; Belcik et al. 2022). There is no comparable information on the Western Grass Snake *N. helvetica* whereas the Digenian trematode *Leptophallus nigrovenosus* has been found in the Ibero-Maghrebian Grass Snake *N. astreptophora* (Navarro et al. 1987).

Adult Grass Snakes typically flee by the approach of a potential predator, with the fleeing distance being rather short (Schleich et al. 1996). When cornered without a reasonable escape option, a Grass Snake may coil the body and hide the head in the center or under a body coil, or flattens the entire trunk, and transforms the head into a triangular shape by displacing the quadrate bones. It may hiss loudly and strike with a closed mouth in an example of Batesian mimicry of coexisting *Vipera* species (de Solan et al. 2020), but they rarely bite (Kabisch 1999; di Nicola et al. 2023). Some individuals even raise their forebody and may also spread their necks horizontally like cobras (Schweizer 1911 cit. in Kabisch 1999; Pokrant et al. 2017; photos in turkherptil.org). The throat can also be inflated vertically, and even open mouth striking or biting has been observed but is extremely rare (Kabisch 1999; authors unpubl. data). If these behaviors do not deter the potential predator, a Grass Snake begins to simulate death by adopting a state of thanatosis (faking death) by becoming limp, open its mouth and let their tongue hang out, sometimes enhancing the deterrence effect by mouth bleeding; often also turning on their back to display the contrasting black and white belly (Eckstein 1993; Kabisch 1999; Malkmus and Sauer 2013; our unpubl. data). When handling Grass Snakes, they often regurgitate their stomach content, emit an obnoxious fluid from their anal glands, and sometimes defecate.

Figure 28.8: Natural color pattern variation of Ibero-Maghrebian **Grass Snakes** (*Natrix astreptophora*) **from: A), B) and G) southern France; C) northwestern Spain; D) northern Morocco; E) Portugal; F) northern Spain. Photo credit: A), B), G) Konrad Mebert; C) and F) Octavio Jiménez-Robles; D) Abdellah Bouazza; E) Benny Trapp.**

The white-orange collar band may function as an anti-predator mechanism by mimicking aposematically colored unpalatable insects (Madsen 1997). In northwestern Spain large toads *Bufo spinosus* avoid juveniles of *N. astreptophora* that display the striking collar pattern (Galán and Fernández-Arias 1993). Finally, defensive behaviors occur at lower body temperatures, while aggressive behaviors are more common at higher body temperatures (Eckstein 1993).

Conservation. Grass Snakes have suffered a decline across their entire range, but most severely in densely populated regions of central and western Europe and in landscapes heavily used for agriculture in Europe and west Asia (Blanke et al. 2008). These human-made modifications resulted in habitat fragmentation and the decline of local amphibian populations that

added to the threats of Grass Snakes and justified its listing as threatened in many central European countries.

Other human activities also have very negative consequences. It is well known that many fishermen kill these snakes due to their fear of these semi-aquatic snakes competing for fish. High mortality caused by traffic, especially when roads cross traditional migration corridors near water, is also an important source of snake decline (e.g., Ioannidis and Mebert 2011; Gezova and Jablonski 2018). Gruschwitz et al. (1993) included seven studies, and Blanke et al. (2008) produced a complete summary with 24 articles on primarily conservation aspects of *N. natrix* and *N. helvetica* from Germany, Netherlands, Switzerland, and Cyprus. They proposed a 4-step-concept species action plan: 1. basic investigations on historical and present distribution/habitat; 2. protection and management of existing populations, including maintaining and improving foraging, oviposition, and hibernation sites; 3. re-establish former distribution (where possible) by constructing corridors between isolated populations, and potentially support weak populations by head-starting with captive-reared snakes; 4. conduct ongoing monitoring. For the Western Grass Snake *N. helvetica* a study by Meister et al. (2012) suggested that conservation actions in landscapes altered by humans should focus on maintaining a habitat mosaic with anuran breeding ponds and adequate oviposition sites. Luckily, in most regions where it is still present, the Grass Snakes are considered a common snake species and accordingly listed with the IUCN category Least Concern. However, the status of the Eastern Grass Snake (*N. natrix*) populations along its southeastern borders in some Asian countries is very poorly known (Iraq, Lebanon, Mongolia, or Turkmenistan; Afrasiab et al. 2011; Asztalos et al. 2020). Also, the Critically Endangered Cyprus Grass Snake is at risk of extinction, despite some recent new findings (Blosat 2008; Zotos et al. 2021).

Alien Grass Snakes may negatively impact the conservation of native populations like the Eastern Grass Snake *N. natrix* that were introduced into indigenous populations of *N. helvetica* in the Netherlands, where they likely hybridize (van Riemsdijk et al. 2020). More examples of alien Eastern Grass Snakes introduced or accidentally translocated into local native Western Grass Snake populations in England, France, Italy, and Germany can be found in Asztalos et al. (2021c) and Griesbaum and Pacher (2024). In addition, there are two locations in Switzerland where alien *N. natrix* were introduced into native populations of *N. helvetica* and have persisted there through decades. In the first location in western Switzerland the alien *N. natrix* hybridized with the native *N. helvetica* (Dubey et al. 2017). In contrast, no such introgression was found between these Grass Snake species in the second location, in central Switzerland (Kieffer Merki et al. 2018).

Natrix astreptophora is not listed in the global IUCN red list but is categorized as Least Concern in Spain and Portugal (Santos et al. 2002; Cabral et al. 2005), and as Near Threatened in Morocco (Pleguezuelos et al. 2010). Within the Iberian Peninsula, threats differ by region; in the northern belt, the species is rather abundant and not threatened (Galán and Fernández-Arias 1993; Santos 2008). However, in northeastern Spain, its presence is negatively influenced by the presence of alien fishes (Escoriza 2018). In central and southern Iberia, the populations are much smaller and survive in ever fewer water bodies that are often heavily degraded (Santos et al. 2002). Consequently, the number of records of the Ibero-Maghrebian Grass Snake in the last 40 years decreased by half in Spain and by even two thirds relative to the number of non-snake reptiles in Languedoc-Roussillon, southern France, suggesting upgrading its current IUCN threat category under the A2 criterium of the red listing process (Santos et al. 2022). In northern Morocco, most of the populations are restricted and isolated to mountainous areas and experience high

vulnerability to climate change (Martínez-Freiría et al. 2013; Escoriza and Ben Hassine 2017). In Algeria, the popu-lations are also threatened by drastic degradation and loss of their aquatic habitats (Beddek 2017). The fungal pathogen *Ophidiomyces ophidiicola*, that causes snake fungal disease, has been documented in this species (0.6% of pathogen prevalence; Blanvillain et al. 2022, 2024; Stark 2024). Finally, populations of *N. astreptophora* are genetically more diverse than those of the more northern species Grass Snakes (Kindler et al. 2018a, b), something well known for Western Palearctic species whose range was affected by the Quaternary glaciations; this represents an added value for the conservation of *N. astreptophora*.

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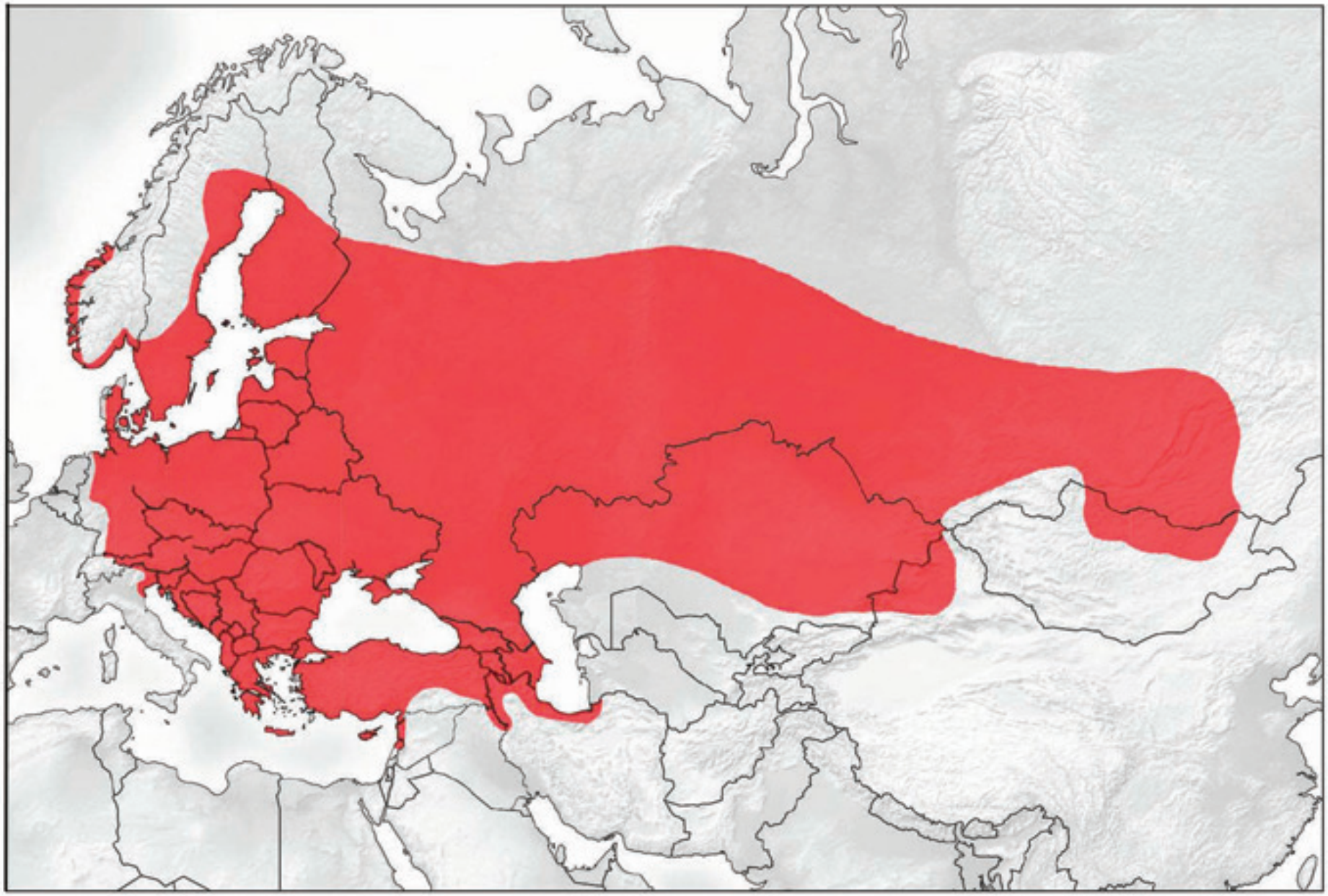

Figure 28.3. The distribution of the Eastern Grass Snake *Natrix natrix*.

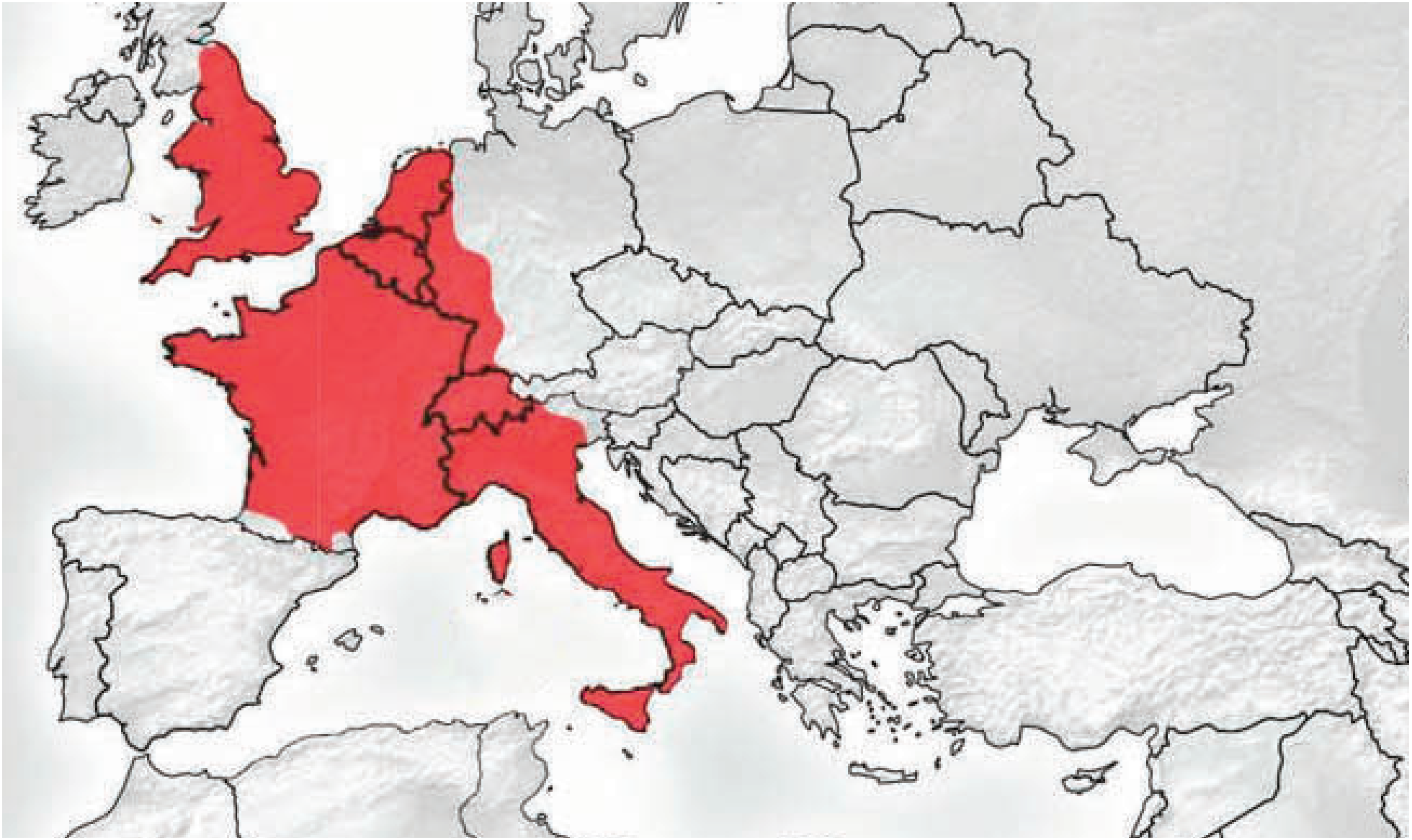

Figure 28.4. The distribution of Western Grass Snake *Natrix helvetica*.

Figure 28.5. The distribution of the Ibero-Maghrebian Grass Snake *Natrix astreptophora*.