Historia Natural

Hybridization between *Natrix astreptophora* and *Natrix maura*: potential cases from Andalusia, Spain

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Resumen: Se conoce que *Natrix astreptophora* y *Natrix maura* habitan en simpatría en una amplia distribución que va desde el sur de Francia a casi la totalidad de la península ibérica, y de Túnez a Marruecos en el norte de África. No obstante, no se conocen híbridos en la naturaleza, posiblemente una muestra de su relativa gran distancia genética. En la presente nota, describimos e ilustramos tres especímenes del oeste de Andalucía, sur de España, que muestran una fuerte evidencia de hibridación con una mezcla de caracteres, algunos intermedios y otros típicamente encontrados en una u otra especie. Estos especímenes representarían los primeros posibles híbridos conocidos entre estas especies de culebras de agua.

Within the Colubridae family, the *Natricinae* subfamily is a large clade that groups more than 250 species, being considered by some authors as its own family Natricidae (Vidal *et al.*, 2007; Pyron *et al.*, 2011; Speybroeck *et al.*, 2020; Deepak *et al.*, 2021). The genus *Natrix* is the Western Palearctic representative of this large lineage of snakes, characterized by their aquatic habits and their predilection for prey associated with aquatic habitats. Recent phylogenetic studies by Kindler *et al.* (2017a, 2017b) have elevated two subspecies of the former monotypic European Grass Snake *Natrix natrix* (Laurenti, 1758) to the species level, the Iberian Grass Snake *N. astreptophora* (Seoane, 1885) and the Western Grass Snake *N. helvetica* (Lacépède, 1789), leaving the third, nominotypic species as Eastern Grass Snake *N. natrix*. These three Grass Snake taxa, together with the Viperine Snake *Natrix maura* (Linnaeus, 1768) and Dice Snake *Natrix tessellata* (Laurenti, 1768), form the five species currently recognized in this genus (Uetz & Hošek, 2021).

Hybridization between species of the genus *Natrix* have rarely been reported. Mebert *et al.* (2011) and Moravec (2015) documented three distinct cases of natural hybridization between *N. natrix* and *N. tessellata* in the Czech Republic and northeastern Italy. Furthermore, hybridization between the closely related Grass Snake species *N. helvetica* and *N. natrix* have been documented through morphological and molecular analyses in their zone of contact in Germany (Kindler *et al.*, 2017a; Schultze *et al.*, 2019). Similarly, and also supported by molecular studies, a few cases of hybridization between *N. astreptophora* and *N. helvetica* have been found in southern France (Pokrant *et al.*, 2016; Asztalos *et al.*, 2020). Natural hybridization with the remaining taxon, *N. maura*, are hitherto not known, and was reported only from captivity between *N. maura* and *N. tessellata* (Klinge, 1925), whereas Mertens (1964) observed copulations between captive *N. maura* and *N. tessellata*. One possible reason for the rarity of hybrids involving *N. maura* possibly origina-

tes in its distant relatedness to the other *Natrix* species, as molecular research revealed that the Grass Snake, *N. natrix sensu lato*, and *N. tessellata* represent sister species (closest relatives), whereas *N. maura* occupies a more basal (older) position in that genus (Guicking *et al.*, 2006). In contrary to perceived rarity of interspecific *Natrix* hybrids, a just published study showed that hybridization between eastern *N. natrix* and *N. tessellata* is more common and widespread than expected (Asztalos *et al.*, 2021). Based on nuclear DNA markers the authors found between 3–4% admixed individuals (27 hybrids from 21 different localities), primarily later-generation-backcrosses, possibly originating from a single hybridization event generations back. These backcrossed hybrids were originally all classified as pure *Natrix* sp. This study exemplifies that hybridization between more distant (11.5% cyt *b* gene) *Natrix* clades occurs regularly (Asztalos *et al.*, 2021).

Three species of the genus *Natrix* occur on the Iberian Peninsula. The Iberian Grass Snake *N. astreptophora* is distributed throughout the region with a higher density of citations in the north and becoming rare towards the south, with no reports in the dry southeast of the peninsula. The Viperine Snake *N. maura* also occupies the entire peninsula, becoming rarer towards the cool northwest. The Western Grass Snake *N. helvetica* is only cited in the Aran Valley (geologically not considered part of the Iberian Peninsula) and in Irun, near the border with France (Pleguezuelos *et al.*, 2002; Asztalos *et al.*, 2020; Salvador *et al.*, 2021).

Natrix maura and *N. astreptophora* are widely sympatric and even live in syntopy. Although the adults of *N. astreptophora* often can be found at a relative distance from aquatic sources and do not appear to be as dependent on water as the adults of *N. maura*, we have found both species together across the entire Iberian Peninsula and in northern Morocco. Similarly, juveniles can often be seen sharing the same habitat. Despite this, the existence of hybrids between both species remains elusive, while Guicking *et al.* (2006) even suggested that natural hybridization between them cannot be achieved.

The dorsal and lateral pattern of *N. astreptophora* is characterized by dark markings separated by 2–3 scales, particularly visible in the contrastingly-marked juveniles and subadults, but normally becomes reduced to small blotches of 2–3 scales width in adults and may even fades away to result in completely patternless, fully grown specimens. There is usually a light-colored (white or yellowish) blotch on the lateral side of the neck, often forming a collar around it, which is posteriorly bordered by a large and black translateral band or bi-lateral angles, often pointed posteriorly. The light-colored blotch is replaced by the general grayish, brownish or rusty body color in adult specimens, and even the posterior black border can disappear, leaving an individual that resembles the similarly brown to gray-colored Montpellier Snake *Malpolon monspessulanus*, a powerful large apex predator which the Grass Snake potentially mimics (authors, pers. obs.). Each ventral blotch often has a smooth, concave edge, and increases in size posteriorly. In Andalusia, all the analyzed specimens had 19 mid-body dorsal rows. The head is larger and vertically more rounded (convex and/or downward bent) with a stouter snout (shorter straight-lateral distance between nostrils and tip of rostral scale) than in *N. maura*. The relatively large eyes are characterized by a broad iris expanding up to edge of the visible eye, primarily reddish (some cream or yellow) in color with a black patch crossing diagonal over the lower anterior portion of the iris, and sometimes

a smaller black patch on the opposite side (upper posterior) of the iris (Figure 1). The supraocular scales are laterally protruding and give their eyes the appearance of a mean and intimidating look, much like in *M. monspessulanus*, and unlike the eyes in *N. maura*. With some exceptions, the supralabials are almost entirely in light color tones, separated from each other by black lines that contrast with the gray-greenish-brown color of the anterior head. *Natrix astreptophora* exhibits one preocular and usually three, rarely two postoculars, and the nostrils are located on the sides of the head (González de la Vega, 1988; Braña, 1998; Speybroeck *et al.*, 2016; Pleguezuelos, 2018).

In comparison, *N. maura*, with the exception of specimens with a bilineata pattern, is characterized by having a dorsal pattern consisting of dark bi-lateral blotches mostly between 3–5

Figure 1: Left (l.) column *Natrix maura*; right (r.) column *Natrix astreptophora*. Top row from France: both specimens from Paziols, France. Photos Konrad Mebert; middle row from Spain: Granada (l.) and La Coruña (r.). Photos O. Jiménez-Robles; bottom row from Morocco; Casablanca (l.) Photo A. Bouazza, and Moulay Abdeslam (r.) Photo G. Martínez del Mármol.

Figura 1: Columna izquierda (i.) *Natrix maura*; columna derecha (d.) *Natrix astreptophora*. Hilera superior de Francia: ambos especímenes de Paziols, Francia. Fotos Konrad Mebert; hilera del medio de España: Granada (i.) y La Coruña (d.). Fotos O. Jiménez Robles; hilera inferior de Marruecos; Casablanca (i) Foto A. Bouazza y Moulay Abdeslam (d.) Foto G. Martínez del Mármol.

scales wide and separated by 1–2 scales, more or less well defined and alternating, often forming a zigzag or slalom-shaped vertebral band in some parts. Its lateral blotches consist of ocelli (dark circular shaped with a light or dorsum-colored center), whereas those of adult *N. astreptophora* are solid black and small. Ventral blotches often are more rectangular or squarrish with irregular edges compared to those in *N. astreptophora*. It usually has 21 rows of dorsal scales in the middle of the body. The head of *N. maura* is elongated and triangular, appears edgier in shape (canthus rostralis) and a straighter and shorter snout than in *N. astreptophora*. Its characteristic eyes appear less extended, smaller in relation to the head than in *N. astreptophora*. In contrast to the orange-reddish iris in *N. astreptophora*, the iris in *N. maura* is lighter, usually orange or cream colored. It contains a second black, irregularly-edged concentric ring surrounding the pupil with variably-shaped orange to cream-colored small flecks or speckles. The thin area between the second ring and the edge of the eye is filled again with the light iris color (Figure 1). The concentric black ring renders the Viperine Snake an appearance of wearing glasses. In some specimens, the ring can be interrupted at one or two positions (example in photo upper left, Figure 1). The supraocular scales are smaller than in *N. astreptophora*. Some specimens have the supralabials with light tones on their lower half, but with the edges being stippled with the same dark (brown, olive, rusty) color as the rest of the head, and not solid black as in *N. astreptophora*. It normally has two preoculars (10–28% in southern Spain exhibit one preocular; Schätti, 1982; Pleguezuelos *et al.*, 1986) and two postoculars, and its the nostrils pointing more upwards than in Grass Snake (González de la Vega, 1988; Braña, 1998; Schätti, 1999; Santos, 2015; Speybroeck *et al.*, 2016).

In this article we document the possibility of hybridization between specimens of *N. astreptophora* and *N. maura* based on the morphological description of three specimens found in nature in southern Spain, part of the Iberian Peninsula. The three specimens, which at first glance were identified as *N. astreptophora*, presented some features of head shape and color pattern that are characteristic of *N. maura*, inclining us to consider them as hybrids between these species.

On March 3th, 2000, during a herpetological expedition through Andalusia, several snakes were rescued that were trapped in a large pool in the municipality of La Rinconada, Sevilla province (30S TG4546, 27 masl). All were identified as *N. maura* except for one specimen, which was initially identified as *N. astreptophora*, but after a closer examination was found to deviate substantially in morphological characteristics (Figure 2). It was an adult male with a total length of 73.7 cm (56.5 cm SVL and 17.2 cm tail), with 19 rows of dorsal mid-body, 157 ventral and 73 subcaudal scales. These ventral/subcaudal scale numbers are within the overlapping values between *N. maura* and *N. astreptophora* from southern Spain, which range between 157–162 ventral and 62–77 subcaudal scales for males (*N. maura*, n=81; *N. astreptophora*, n=15, unpublished data by JPGV). Hence, they could represent either of both, a normal species-specific expression or an intermediate value between the two watersnakes. The dorsal pattern is very contrasting with black blotches on light-gray body color, generally reminiscent of young *N. astreptophora*, but it consists also of relatively wide, translaterally often fused, black blotches which is untypical for adult *N. astreptophora* of that size and also uncommon in their juveniles. A few

Figure 2: Perceived likely hybrids between *Natrix maura* and *N. astreptophora* from southern Spain based on a mixed expression of morphological characters. a) La Rinconada, Sevilla; b) Teba, Málaga; c) Municipality of Huelva, with the colored lines indicating characters typical for one or the other species; red line for *N. astreptophora*: 1) light supralabials with vertical black lines, 2) reddish iris, 3) light collar band, with 4) black triangular blotches adjacent posteriorly, 5) three postoculars, 6) no zigzag or slalom dorsal band, and blotches separated by 2–3 scales, 7) solid black lateral blotches, 8) wide distance up to three scales between two dorsal blotches; blue line for *N. maura*: 9) shorter, edgier head profile, 10) blackish concentric iris ring, 11) elongated triangular head shape dorsally, 12) wide dorsal and lateral blotches of 3–5 scales width, 13) ventral blotches irregularly-edged, non-concave, 14) not increasing in size posteriorly, latter two characters not visible on photo. See also the text for elaborations on above characters.

Figura 2: posibles híbridos reconocidos entre *Natrix maura* y *N. astreptophora* del sur de España basado en una mezcla expresiva de los caracteres morfológicos. a) La Rinconada, Sevilla; b) Teba, Málaga; c) Municipio de Huelva, con las líneas coloreadas que indican los caracteres típicos de una u otra especie; línea roja para *N. astreptophora*: 1) supralabiales claros con líneas verticales negras, 2) iris rojizo, 3) banda de collar claro, con 4) manchas triangulares adyacentes en la parte posterior, 5) tres postoculares, 6) sin banda dorsal en zigzag o slalom, y manchas separadas por 2-3 escamas, 7) manchas laterales negras sólidas, 8) amplia distancia hasta tres escamas entre dos manchas dorsales; línea azul para *N. maura*: 9) perfil de cabeza más corto y afilado, 10) anillo de iris concéntrico negruzco, 11) forma de cabeza triangular alargada dorsalmente, 12) manchas anchas dorsales y laterales de 3-5 escamas de ancho, 13) manchas ventrales irregulares con bordes, no cóncavos, 14) no aumentan de tamaño posteriormente, los dos últimos caracteres no son visibles en la foto. Consultar también el texto para obtener más detalles sobre los caracteres anteriores.

isolated dorsal blotches stretch across four scales, a width typical for *N. maura*, whereas the distance of two light scales between consecutive dorsal blotches is intermediate. The shape of the dorsal blotches in this putative hybrid approach those expressed in some *N. maura*, however, it is missing the formation of a partial longitudinal zigzag band typical of that species. The ventral pattern is also intermediate, exhibiting concave-edged blotches and also irregular blotches. The head resembled more that of *N. maura*, including elongated shape, a second black ring in the cream-colored iris, one (left) and two (right)

preocular and two postoculars on each side of the head (Figure 2). However, the grey collar band, same as in the ground color, and the posteriorly bordered black transversal band, as well as the black supralabial bars are typical for *N. astreptophora*.

On May 1st, 2014, in the municipality of Teba, Málaga province (30S UF3096, 496 masl) another specimen was found crossing a road. We do not have data on its body pholidosis, sex or length. We estimate that it was a hybrid between *N. astreptophora* and *N. maura* because it showed eyes similar to *N. maura* (Figure 2), but possessed a mixed body pattern. It consists of a row with wide translateral blotches over its back, apparently reflecting the fusion of the commonly observed two bilateral rows of dorsal blotches. This and the four-scale wide lateral blotches are characters common in *N. maura*, but rare and only in juveniles of *N. astreptophora*, whereas the complete lack of lateral ocelli and the missing of a partial dorsal zigzag or slalom band is typical of *N. astreptophora*. The ventral black blotches exhibit a mix between straight and concave, but often dissolved, edges without increasing in size posteriorly, resembling an intermediate status between *N. astreptophora* and *N. maura*. Postoculars three and preoculars are representative of *N. astreptophora*. The supralabials were of very light color and delimited by black lines that clearly contrasted with the anterior color of the head, an exclusive characteristic of some specimens of *N. astreptophora*, as well as the combination of three postoculars and one preocular (Figure 2).

A third specimen was observed on May 7th, 2018 in the municipality of Huelva (29S PB8830, 8 masl). It was found in some red fruit crops and was stunned from having been beaten by some farmers, while another called one of the authors to relocate it to a safe place. It was an adult male, 69.5 cm in total length (52.5 cm SVL and 17 cm of tail), with 19 rows of dorsal scales in the middle of the body, 164 ventrals and 80 subcaudals, which represent the values for *N. astreptophora* and are just a little higher than the overlapping range between both natricine snakes (see above). This specimen generally resembled the putative hybrid in Figure 2. For example, the translateral black blotches on the back are separated by 2–3 light scales as is typical in *N. astreptophora*, but most blotches are fused transversally, a character known from *N. maura* and occurs only rarely in juvenile *N. astreptophora*. The black blotches on the venter are mostly irregularly-edged, non-concave, and not increasing in size posteriorly as in *N. maura*. The head was triangular-elongated with straight and short snout as in *N. maura* but the cephalic pholidosis (one preocular and three postoculars) is typical of *N. astreptophora*. The supralabials are separated by black lines that contrast with the anterior color of the head, which does not occur in *N. maura*. The additional black iris ring has orange markings as in *N. maura* and is also missing the black diagonal, anterior iris-patch so typical for *N. astreptophora*. The supraocular scales are slightly larger than in *N. maura* but apparently smaller than is typical for *N. astreptophora* (Figure 2). This mix of characters from two *Natrix* species render this specimen as a likely hybrid between them.

Natrix astreptophora is a species that requires high humidity. For example it can be quite abundant in the cooler, wetter northern Iberian Peninsula (Galicia, Asturias, Cantabria, north of Burgos and Léon), whereas the Iberian Grass Snake is generally much scarcer in the Mediterranean region and the majority of records

originate from mountain and coastal areas. Specifically, in the hot and dry climate of Andalusia, after more than 30 years collecting reptile data, we can affirm that it is one of the rarest species of snake in this region, only second to the Smooth Snake *Coronella austriaca*. We presume that this rarity reflects the observed low density of the Iberian Grass Snake which could lead its males to mate with the overabundant Viperine Snake when not finding conspecific partners (JPGV, pers. obs.). Similarly, interspecific breeding in European vipers was likely promoted by the rarity of one parental taxa or a low operational sex ratio (e.g., Mebert *et al.*, 2015; Guiller *et al.*, 2017). In addition, the specimens were found in anthropic environments, where *N. astreptophora* may be even rarer, as noted by Pleguezuelos & Feriche (2003).

While cases of hybridization in snakes are becoming better known and can take the form of stably admixed populations with a cyto-nuclear discordance (different origin of mt- and nDNA, e.g. Doniol-Valcroze *et al.*, 2021), specimens based on a fresh hybridization event (F1-hybrids resulting from the copulation between two distinct species) remain rare. Without genetic data, it is difficult to assess their hybrid status. However, one can still assess whether an unusual specimen represents a rare hybrid or an aberrant specimen, based on the composition of its morphological features and their mode of expression/inheritance.

Abnormal morphology caused by the mutation in one gene usually affects the expression of one character only and not several apparently unlinked external characters, as for example up to 14 in our three *Natrix* specimems. In Figure 2c, we listed eight characters that are associated with (or are more common in) *N. astreptophora* and five characters typically found in *N. maura*. Such a combination of characters of different origins can not share a common genetic basis and, hence, renders it extremely unlikely that these *Natrix* specimens represent simply unusual morphs of a locally known species.

In contrary, the expression of these 14 characters from two related and sympatric/syntopic species speaks strongly for F1-hybrids, and with a lower probability for an F2- or later-generation backcross (Mebert, 2008, 2010). This concludes that the expression of morphological traits follows the common Mendelian genetic system, be them alleles of dominant-recessive or co-dominant inheritance. Hence, morphological traits in a F1-hybrid show an expression of either (a) one of the parental species, or (b) an expression intermediate between those of the parents (Mebert *et al.*, 2020). This is indeed possible herein, as illustrated in Figure 2. Furthermore, a study conducted across a large hybrid zone of related watersnakes, *Nerodia sipedon* and *N. fasciata* (Mebert, 2008, 2010) revealed more than 20% of snakes with a hybrid phenotype (based on 40 morphological characters), of which all individuals proved to exhibit also a hybrid genotype, hence, leading to a simple statement: "if it looks like a hybrid, it is a hybrid". In conclusion and with a closer look, using a multitude of morphological variables, the intermediacy of dorsal pattern and the mix of bi-parental head characters from two *Natrix* species discussed above and exhibited in Figure 2 are strong indicators for F1-hybrids status. Hence, the three specimens likely represent the first known natural hybrids between *N. astreptophora* and *N. maura*, yet, we recommend to test the genetic composition of similar admixed specimens that might be discovered in the future.

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Incubación, nacimiento y comportamiento de *Homonota horrida* (Squamata: Phyllodactylidae) en cautiverio

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El género *Homonota* incluye 12 especies de lagartos de hábitos terrestres y nocturnos que se distribuyen desde el sur de Bolivia, Argentina, oeste de Paraguay, Uruguay y el estado brasileño de Rio Grande do Sul (Morando *et al.*, 2014). *Homonota horrida* (Burmeister, 1861) se encuentra presente en Paraguay y en gran parte de la Argentina (Cacciali *et al.*, 2017; Cabrera *et al.*, 2018). Su ciclo reproductivo es anual y se inicia en primavera (Aun & Martori, 1994; Cruz, 1994; Nieva *et al.*, 2013); la oviposición ocurre desde octubre a enero (Kretzschmar & Abdala, 2001). De acuerdo con los menores tamaños de neonatos y juveniles los nacimientos ocurrirían durante la primavera y el verano (Cruz, 1994; Nieva *et al.*, 2013).

El estado de conocimiento acerca del período de incubación y eclosión en *H. horrida* es escaso, pero Cacciali *et al.* (2007) encontraron un huevo de *H.* aff. *horrida* en el Chaco Paraguayo y lo incubaron bajo condiciones de laboratorio; después de aproximadamente seis meses se produjo la eclosión de un neonato con una longitud total de 2,5 cm. Hasta lo que se conoce esta es la única información sobre la incubación y eclosión para esta especie. En este trabajo informamos sobre el tiempo de incubación, la morfometría de la cría y el comportamiento defensivo novedoso del neonato de *H. horrida* en cautiverio.