

Hooding in the dice snake *Natrix tessellata* may backdate the origin of such behaviour in the genus *Natrix*

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Hooding is a very well-known defensive display of snakes, the snake raises its head and the anterior part of the body from the ground, and the neck is dorsoventrally compressed by lateral expansion of the cervical ribs (Greene, 1979; Young et al., 2010). This aposematic signal is intended to intimidate potential predators or threats, and has been made famous in popular culture by cobras (family Elapidae) although its use is not restricted to elapid snakes (Pope, 1935; Gharpurey, 1954; Greene, 1979). Among others, it has been recorded in three natricid snakes of the genus *Natrix*: *Natrix natrix*, *Natrix helvetica* and *Natrix astreptophora* (Kabisch, 1978; Pokrant et al., 2017; Paterna, 2019). In 2017, Pokrant et al. concluded that this defensive mechanism is a ‘fossil’ behaviour, inherited by the grass snakes from an ancestor that lived in Europe until the Miocene–Plio–Pleistocene, which had evolved hooding as Batesian mimicry of sympatric elapids. Besides apparently sharing this defensive display with cobras, *Natrix* species also visually imitate sympatric viperids in both dorsal pattern, defensive behaviour and by head triangulation (Valkonen et al., 2011; Paterna, 2019).

In this study we describe hooding in two dice snakes *Natrix tessellata* (Laurenti, 1768). The first observation was on 3 May 2006 along the Chienti river, in the locality of Bistocco di Camerino, in the Marche region, Italy, where there is a well-established population of dice snakes. On this occasion, a specimen of a total length of about 105 cm, raised its neck and spread a hood while the posterior portion of its body was being held by one hand (Fig. 1A & B). This performance lasted long enough for the snake to be photographed from several different angles. The maximum width reached by the lateral expansion of the neck was approximately equal to the length of the specimen’s head, and stretching of the neck revealed dark-pigmented skin between the dorsal scales. This manoeuvre also accentuates the head triangulation of the specimen, in a similar manner to that observed in congeneric and sympatric *N. helvetica* (Paterna, 2019). The second episode occurred on 1 April 2008 in the Colfiorito swamp, in the province of Foligno, also in the Marche region, where on the lakeside, a dice snake displayed a hood (Fig. 1C & D) in a similar manner to the previous observation. Furthermore, in both cases the snakes maintained the defensive display even after their necks were returned to the ground and they were in the process of fleeing (Fig. 1B & D). In both episodes there was a marked

dorsal plane variation between vertebrae and ribs (Fig. 1A & C), i.e. the neck didn’t appear completely flattened dorsally as the vertebrae were more ‘elevated’ or ‘externally pronounced’. Despite descriptions of hooding in the grass snakes being rare in literature, the externally pronounced vertebrae does not seem to be so evident in the reported case of *N. helvetica* (Paterna, 2019), but clearly present in *N. astreptophora* which is featured in many photographs on online platforms, to the extent that it seems that hooding could even be frequent in this species.

It seems likely that hooding has a common evolutionary origin in those four *Natrix* species that have been recorded displaying it. The fact that such display has been observed in *N. tessellata*, a sister taxon of *N. astreptophora*, *N. helvetica* and *N. natrix*, but has not been documented in the most basal species *Natrix maura*, allows us to connect the origin of this behaviour into a more precise time range between the divergence of *N. maura* and the last common ancestor for the remaining species. On the basis of recent phylogenetic studies, the development of such behaviour could be placed in the early-middle Miocene (Guicking et al., 2006; Kindler et al., 2018; Schöneberg et al., 2023). This is consistent with the hypothesis that this defensive mechanism may have been evolved as emulation of sympatric elapids in central Europe (Pokrant et al., 2017).

The oldest elapid fossils found in Europe belong to the species *Naja romani*, of which there is an abundance from the early German Miocene (Szyndlar & Schleich, 1993), middle French Miocene and late Austrian Miocene (Szyndlar & Rage, 1990), to a second species, *Naja iberica*, and indeterminate remains of a *Naja* sp. of which records date back to the middle–late Spanish Miocene (Szyndlar, 1985; Villa et al., 2024). To date, the known European fossil records of the genus *Natrix* from the mid–late Miocene belong exclusively to extinct species, such as *Natrix sansaniensis* from France (Rage, 1988; Rage & Auge, 1993; Ivanov, 2002), and *Natrix longivertebrata* in Austria (Bachmayer & Szyndlar, 1985) and eastern Europe (Szyndlar, 1984, 1991), while fossils attributed to the contemporary *N. tessellata* and *N. natrix* have origins no earlier than the late Pliocene and Pleistocene (Markert, 1976; Zerova & Chkjkvadze, 1984; Ivanon, 1999). However, the oldest fossil records of the genus *Natrix* are restricted to central Europe, and date back to the late Eocene and early Oligocene, with



Figure 1. Adult dice snakes *Natrix tessellata* performing the hooding display- **A.** Specimen from river Chienti hooding in erected position, **B.** Same specimen as **A.** hooding while its neck ascends to the ground, **C.** Specimen from the Colfiorito swamp hooding in erected position, **D.** Same specimen as **C.** hooding parallel to the ground.

the species *Natrix mlynarskii* found in France (Rage, 1988; Ivanov, 2001). It is therefore plausible that such defensive mechanism has a central European origin, back-dated to the ancestors of *N. tessellata* prior to the fragmentation in which ancestral populations expanded eastwards, and from which *N. tessellata* evolved in south-western Asia (Rögl & Steininger, 1984; Guicking et al., 2006).

An alternative hypothesis on the origin of this defensive display might not connect this phenomenon to the previous coexistence in the same territory with cobras, but with another defensive mechanism involved in the imitation of viperids. It is noteworthy how hooding in *Natrix* is linked to head triangulation and contributes to its definition and

extension through the lateral expansion of the first cervical ribs (Paterna, 2019). In this genus hooding seems to be generally performed while raising the neck, while other species of colubroids, e.g. *Dasypeltis* and *Heterodon*, usually perform hooding with their neck and head close or parallel to the ground. European viperids, in defensive posture raise their heads from the ground and hiss loudly, while larger allopatric viperids, such as *Bitis* spp. and *Crotalus* spp., in addition to this further triangulate their heads. It is of interest that hooding has not been observed (yet?) in *N. maura*, instead this species, as its common name ‘viperine water snake’ suggests, is very well documented as a viper mimic (Valkonen et al., 2011).

Further investigation of hooding in natricids is required to fully understand its function and origin. If hooding was to be subsequently recorded in *N. maura*, the more ancient of the species considered, then this would influence the temporal and spatial explanations of its origin.

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