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SHORT COMMUNICATION

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Reptile behaviour in natural refuges - 6. Observations from a long-term study of multi-species cohabitation and communal nesting, with links to video evidence

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Communal nesting and refuge sharing among reptiles can reveal the complex dynamics of interspecific tolerance based on temporal niche partitioning and chemically-mediated coexistence (Doody et al., 2009; Mason & Parker, 2010). The system on which this study is based comprises several natural refuges within the same area; however, sustained multi-species co-occupation and communal oviposition have so far only been documented in one primary refuge. The main refuge is a natural rocky embankment in soft marl, with interconnected galleries and several main chambers that have changed gradually over the eight-year study period. Although communal oviposition and shared hibernacula are well-documented in some reptile taxa, long-term co-occupation of a natural refuge by multiple snake species and a large lizard in the wild, particularly in the presence of potential predator-prey relationships, remains poorly documented. The present study therefore provides novel insights into multi-species coexistence under natural conditions. I report observations from an eight-year continuous field study (2018–2025) in north-eastern Iberia, documenting the co-use of a natural refuge by five reptile species: the saurophagous snake *Malpolon monspessulanus*, the ladder snake *Zamenis scalaris*, the natricine snakes *Natrix astreptophora* and *Natrix maura*, and the lizard *Timon lepidus*. A key finding is the consistent use of the refuge as a shelter and communal nesting site. All species deposited their egg clutches within the chambers of the refuge. Furthermore, neonates of all species, including the two natricines and *T. lepidus*, have been documented emerging from this shared nursery, indicating successful incubation and highlighting the critical role of the refuge in reproduction. This is a rare case of long-term multi-species reproductive coexistence. Such assemblages offer valuable insight into behavioural flexibility, chemical communication and habitat-driven ecological interactions. They also illustrate Valverde's (1967) concept that essential physical structures can act as nuclei for Mediterranean vertebrate communities, here exemplified by a single refuge supporting multiple reptile species.

The refuge's significance was first documented by Serrano-Fochs (2019), and subsequent observations have revealed a network of behaviours including courtship, oviposition and nuanced interspecific interactions detailed in five previous publications and illustrated with numerous video clips filmed either within or just outside the refuge (Serrano-Fochs, 2026a; 2026b; 2026c; 2026d; 2026e).

Figure 1. Three adult female snakes in the refuge together illustrating interspecific tolerance, *Malpolon monspessulanus* (left), *Natrix astreptophora* (centre) and *Zamenis scalaris* (right)

The five species show distinct but overlapping patterns of refuge use mostly during the spring-summer reproductive period and again when hatchlings emerge. *Timon lepidus* is the most constant user, occupying and maintaining the refuge year-round, often navigating a delicate risk balance when laying eggs in the same chambers as snakes, since both adults and neonates could be predated (BHS video, 2026a). *Malpolon monspessulanus* and *Z. scalaris* are regular breeders, using the refuge for courtship and oviposition. Despite some competition for space, with *Z. scalaris* being more territorial and occasionally displaying behaviours such as tail-lashing, frontal confrontation, pursuit and head pushing (BHS video, 2026b), these two colubrids exhibit remarkable mutual tolerance, including direct contact, with spatial and temporal overlap observed during courtship and copulation (Serrano-Fochs, 2026b). Interestingly, males of *M. monspessulanus* have been observed sharing the same chambers for resting and sleeping, showing direct conspecific contact without aggressive encounters, despite the species being described as combative among males. A

female *N. astreptophora* is a frequent and pacific occupant, cohabiting peacefully with *Z. scalaris* and *N. maura*, although it generally avoided *M. monspessulanus*, it also showed tolerance of it (Fig. 1). Whereas *N. maura* is less frequent, some females have been recorded, and their neonates have been documented emerging from the refuge.

The foundational element of this community is the ocellated lizard, *T. lepidus*. Its role extends beyond being a simple occupant and instead functions as an ecosystem engineer. The lizards' activities in digging, maintaining and clearing the chambers create and preserve the microhabitat structure essential for all other species (Serrano-Fochs, 2026c). Without this ongoing maintenance, the quality and likely the very existence of this shared refuge would be compromised. The lizard's tolerance and indirect custodianship facilitate the refuge's function as a multi-species reproductive hotspot.

Within the refuge, both conspecific and heterospecific aggregation patterns vary by species and reproductive stage. Conspecific aggregation is most evident during courtship (BHS video, 2026c & BHS video, 2026d), while heterospecific aggregations occur during courtship and post-copulation, particularly among females preparing to oviposit. *Malpolon monspessulanus* neonates form dense aggregations by clutch, whereas aggregations of other species are not observed outside the chambers, possibly remaining clustered within. In all snake species, dispersal occurs shortly after the first ecdysis and all show tolerance of heterospecifics. *Timon lepidus* has been observed approaching the snakes neonates without aggressive or predatory interactions (BHS video, 2026e). These patterns align with adaptive hypotheses of aggregation, including attack abatement, maternal benefits and thermal and hydric egg insulation (Doody et al., 2009). Repeated use of high-quality refuges can create reproductive hotspots where aggregations form not only during mating but also at oviposition (Graves & Duvall, 1995) and hatchling emergence. Natal philopatry and maternal nest-site fidelity may further reinforce such patterns (Brown & Shine, 2007), making this multi-species refuge functionally analogous to communal nesting systems described in other reptiles (Mateo & Cuadrado, 2012). I extend them by documenting heterospecific aggregations, reflecting complex behavioural and chemical co-ordination among species (BHS video, 2026f), with females and males attracted not only by conspecifics but also to other species, recognising the refuge as an optimal reproductive site (Mason & Parker, 2010). Aggregation is dynamic: in 2021, predator presence, possibly a fox, led females to aggregate defensively within the refuge. Whereas in 2025, disturbance by a domestic cat prompted a female *M. monspessulanus* to relocate to a secondary refuge already used by other snakes, likely guided to it by heterospecific chemical cues. These observations illustrate the behavioural flexibility and social-chemical co-ordination underpinning coexistence in this multi-species system.

Chemical cues likely play a central regulatory role. Reptiles use skin lipids, cloacal secretions and substrate-borne chemical trails for species recognition, reproductive signalling and prey identification (Mason & Parker, 2010). The observed tolerance suggests a sophisticated level of chemical recognition of life stage and reproductive context, which may temporarily suppress predatory motivation and aggression during critical reproductive phases. Refuge fidelity and the probable use of both conspecific and heterospecific cues likely promotes coexistence during this critical reproductive window. Such chemically mediated behavioural plasticity may be key to the long-term stability of this communal system, supporting theoretical models where reproductive benefits and cue-based recognition can override immediate predatory impulses in high value sites (Doody et al., 2009). This pattern reflects a broader framework of reptile social behaviour, where chemical communication facilitates both reproductive synchrony and flexible social associations that promote coexistence (Mason & Parker, 2010). These behavioural interactions provide concrete examples of chemical mediation in the refuge. For instance, *T. lepidus* appears to act as a cautious custodian rather than a predator toward *M. monspessulanus* eggs and hatchlings (Serrano-Fochs, 2026c), while *M. monspessulanus* shows inhibited cannibalism toward conspecific neonates (Serrano-Fochs, 2026d). Such interactions are likely regulated by chemical cues, a system also employed during courtship behaviours such as the cloacal rubbing observed in both *M. monspessulanus* and *Z. scalaris* (Serrano-Fochs, 2026b). These observations reinforce the role of chemical communication in modulating tolerance, risk assessment, and reproductive co-ordination within this multi-species refuge.

This short note documents an exceptional multi-species system of ecological complexity. Five reptile species co-occur and share a natural refuge, with tolerance and both conspecific and heterospecific aggregation enabling communal success. *Timon lepidus* acts as a keystone species, facilitating refuge use by other reptiles. Neonates of all species emerge successfully, demonstrating true reproductive success arising from behaviourally controlled multispecies cohabitation rather than simple accidental co-use. These observations highlight the role of high-quality microhabitats in shaping tolerance-based community formation. The long-term stability of this assemblage provides strong support for adaptive hypotheses of communal nesting (Doody et al., 2009), and suggests that such complex shared nesting sites may be more common than previously documented. To my knowledge, this represents the first case in Europe of a long-term, multi-species communal refuge supporting courtship, oviposition and successful hatching of both lizards and snakes, including coexisting predator-prey pairs. Continued monitoring will help clarify temporal dynamics, mechanisms of chemical recognition, aggregation and the potential fitness benefits underpinning this remarkable assemblage. Together, these observations indicate that the refuge supports not only ecological coexistence but also a form of context-dependent sociality in reptiles, mediated by a combination of behavioural and sensory mechanisms.

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