

Reptile behaviour in natural refuges - 5. Refuge choice under predation risk: *Timon lepidus* navigating snake-occupied shelters, with links to video evidence

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Reptiles select refuges by balancing predation risk with shelter quality, thermoregulation and access to resources that refuges may offer (Martín & López, 1999; Amo et al., 2007). Where suitable refuges are scarce, the risk/reward trade-off in their selection becomes especially pronounced. At least in wall lizards *Podarcis muralis*, individuals are known to rely on a combination of chemical and visual cues to evaluate predator presence and refuge safety (Amo et al., 2004a; 2004b), yet how risk is assessed in natural multi-species contexts, particularly when refuges are simultaneously occupied by potential snake predators (the saurophagus Montpellier snake *Malpolon monspessulanus* and non-saurophagus ladder snake *Zamenis scalaris*), and conspecifics, has seldom been documented in the wild. Building upon previous reports from the same communal refuge in north-eastern Iberia that has been monitored for eight years (Serrano-Fochs, 2019; 2026a), the present observations reveal fine-scale risk assessment behaviours by the ocellated lizard *Timon lepidus* in this multi-species refuge context.

Both *T. lepidus* and *M. monspessulanus*, regardless of reproductive state, typically withdraw into the refuge as daylight fades and remain inactive until the following morning. In contrast, *Z. scalaris* are primarily crepuscular/nocturnal hunters but, when gravid, also retreat to refuges in the evening and remain inside throughout the night. The two snake species differ in their diets: reptiles, including *T. lepidus*, are regular prey for *M. monspessulanus* (Pleguezuelos & Salvador Milla, 2021), whereas they are exceptionally rare and insignificant in the diet of *Z. scalaris* (Pleguezuelos et al., 2007). These predictable activity patterns of cohabiting snakes, with differences in lizard behaviour according to lifecycle stage (ontogenetic differences), create a dynamic environment in which *T. lepidus* must constantly evaluate risk and select refuges accordingly. The following observations illustrate how the lizard responds to such complex multi-species scenarios.

In this study, *T. lepidus* exhibited context-dependent and ontogenetic variation in risk assessment, with distinct diurnal and nocturnal strategies observed among both adults and neonates.

Nocturnal risk assessment

During nocturnal monitoring in 2024, an adult *T. lepidus*, likely a gravid female based on morphology and breeding season, was recorded resting at the refuge entrance after all internal chambers were occupied by snakes (BHS video, 2026a). The interior contained gravid females of both *Z. scalaris* and *M. monspessulanus*. Faced with no available unoccupied refuges, the lizard opted to sleep at the entrance rather than abandon the site entirely. Notably, *M. monspessulanus* was observed assessing the lizard but showed no predatory response before retreating deeper into the chamber. Throughout the night, the lizard maintained this exposed position, adjusting its orientation to monitor the snakes through the refuge opening. At one point, the lizard and a *Z. scalaris* came into direct contact at the refuge entrance. The lizard performed a rapid jump to increase distance from the snake but remained in the vicinity. It then exhibited a sequence of tail-waving movements (BHS video, 2026a). Once the snake entered the chamber, the lizard returned to the same spot at the entrance, where it remained for the rest of the night.

Neonates of *T. lepidus* have been recorded in 2024 emerging from the refuge during the late evening and through the night (BHS video, 2026b). After hatching, they exhibit brief exploratory behaviour, including tongue-flicking and limited movement within the refuge, occasionally climbing onto the camera, likely attracted by its mild heat emission. Following this short assessment phase, each hatchling performed an abrupt leap toward the exterior, rapidly dispersing into the darkness.

Diurnal hierarchical threat assessment

During a controlled experimental approach in 2021, an adult *T. lepidus* was forced to choose between a human observer and the refuge occupied by a *Z. scalaris*. The lizard entered the refuge, displaying vigilance, including head-raising, scanning and tongue-flicking, and freezing in response to the snake's movements. When the observer pushed it deeper inside using a camera, the lizard positioned its back to the snake while facing the observer (BHS video, 2026c). When touched by the snake, it reacted suddenly toward the snake, performing tongue-flicking. After the observer retreated, the lizard left the refuge. Once outside, it was startled by the

observer, performed a sudden defensive jump with its mouth open, and quickly escaped to an alternative refuge.

In 2024, on several occasions (28–30 June, during daylight), the lizard approached the refuge while different snake species were present, repeatedly inspecting the entrance and remaining nearby without fleeing. These encounters occurred in late June, coinciding with the oviposition period for both *T. lepidus* and *M. monspessulanus*.

Neonate *T. lepidus* have also been recorded emerging from the refuge during daylight (BHS video, 2026d). In contrast to the almost immediate nocturnal dispersal, they first engage in brief exploratory behaviour within the refuge and occasionally inspect the surrounding environment before leaving the shelter.

Interpretation of observations

All these observations align with previously documented anti-predator strategies in this population of *T. lepidus*, including chemical stealth, tongue-flicking and vigilant scanning (Serrano-Fochs, 2026a). The lizard also adjusts refuge use and alert behaviour according to predator context, integrating multiple sensory modalities and stimuli to evaluate changing risk levels (Amo et al., 2004b; 2005; Mason & Parker, 2010).

The nocturnal behaviour appears to represent a calculated compromise under constrained conditions, where proximity to potential predators is preferred over complete exposure outside the refuge. The interaction illustrates refined risk assessment, as the lizard may detect reduced predatory motivation of gravid snakes, possibly through chemical cues reflecting the predator's physiological or motivational state, a phenomenon documented in other reptiles (Mason & Parker, 2010; Martín & López, 2014). This is an exceptional case, as other lizards prioritise predator-free refuges over potential thermal gains (Amo et al., 2004c), emphasising that risk of predation is probably the dominant factor in the rejection of a particular refuge. In the current study, the lizard's risk assessment appears to integrate thermoregulatory benefits with reproductive and protective needs, suggesting tolerance thresholds may be modulated by temporal partitioning and the limited availability of optimal refuges, an adaptive trade-off consistent with cost-benefit frameworks for reptile behaviour (Doody et al., 2009). Overall, this behavioural adjustment allows the lizard to balance safety with access to suitable refuge resources, discriminating between threat levels and showcasing a sophisticated, multifactorial decision-making process (Amo et al., 2004b).

When facing *Z. scalaris*, *T. lepidus* exhibited a tail-waving display that may represent either a startle response or a controlled pursuit-deterrent display. In the latter case, the movement would communicate to the predator that it has been detected ('I've seen you') and good physical condition to the predator. Such honest displays reduce the element of surprise and discourage attack by indicating that the prey is alert and capable of escape (Martín, 2002; Eifler & Eifler, 2010).

Daylight encounters reveal hierarchical and context-dependent threat assessment. In the experimental human approach, *T. lepidus* chose to enter a refuge occupied by *Z. scalaris* demonstrating that snakes represent a predictable,

manageable risk compared to unpredictable threats. Prior recognition of *Z. scalaris* as non-saurophagous likely contributes to the lizard's responses (Amo et al., 2004a; Serrano-Fochs, 2019). The lizard also approached active *M. monspessulanus* individuals during daylight, showing alertness and situational control, monitoring the snake's movements to ensure a secure escape margin. Together, these responses highlight the lizard's ability to integrate predator identity, immediacy of threat and refuge context when making escape or approach decisions (Amo et al., 2005).

The cognitive and behavioural flexibility of the lizard reflects an adaptive cost-benefit assessment between immediate predation risk and long-term habitat value. Lizards must balance access to refuges against predators such as *M. monspessulanus* that can strongly impact population demography, particularly by predation of females (Belaud et al., 2022). Observed tolerance of a gravid snake illustrates the lizard's ability to assess predatory motivation and adjust behaviour accordingly, demonstrating how persistent threats shape complex interspecific interactions. Such tolerance may also be influenced by reproductive motivation, as gravid lizard females must secure suitable oviposition sites even when predation risk has increased.

Neonate *T. lepidus* exhibit variable emergence strategies that combine brief exploration with abrupt departure from the refuge. Both diurnal and nocturnal hatchlings show tongue-flicking and limited movement within the shelter before performing a sudden leap toward the exterior. However, individuals dispersing in the daytime appear more active and spend longer exploring and visually inspecting the surroundings before dispersal, suggesting enhanced environmental assessment when there is daylight. At present, it remains unclear whether diurnal or nocturnal emergence is the prevailing pattern, or which might offer higher survival rates. In contrast with adults, neonates appear to perceive the refuge itself as a high-risk environment, prompting immediate dispersal. This ontogenetic divergence suggests that what functions as a long-term resource for adults may represent a high-risk environment for hatchlings. Such behavioural polarity may explain the near absence of juveniles in this established refuge across the years.

Although focusing on a single refuge and population, similar cases of *T. lepidus* and *M. monspessulanus* co-occupying shelters occur in neighbouring population and in southern France (Coquis et al., 2025), suggesting this coexistence pattern may be widespread across Mediterranean habitats. This aligns with the role of *T. lepidus* as an ecosystem engineer capable of modifying and maintaining refuge structures (Serrano-Fochs, 2026b).

Conservation significance

Interspecific interactions mediated by chemical cues, and context-dependent behavioural responses are fundamental not only for understanding behavioural ecology but also for applied conservation. Introduced predators can devastate lizard populations lacking evolved anti-predator experience, as seen with the invasive *Hemorrhois hippocrepis* on the endemic *Podarcis pityusensis* in the Balearic Islands, and by

Lampropeltis californiae on endemic *Gallotia stehlini* in the Canary Islands. The articles in this series demonstrate that *T. lepidus* has the capacity to evaluate risk and adjust behaviour to minimise predation, highlighting the potential for using behavioural conditioning in conservation management to reinforce recognition of predatory species and reduce stress in refuges under novel predation pressures.

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