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SHORT COMMUNICATION

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Nocturnal mass foraging by semi-aquatic natricine snakes linked to the spawning behaviour of the Prespa bleak *Alburnus belvica* in Lake Prespa, with links to video evidence

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The behaviour patterns of animals are not necessarily fixed and may be modified by factors such as food availability, predation risk, interspecific competition and environmental temperature (Carothers & Jakšić, 1984; Metcalfe et al., 1998; Kronfeld-Schor & Dayan, 2003; Fraser et al., 2004). Within this context, European natricine snakes, although primarily considered diurnal or crepuscular, may be opportunistic foragers at night when elevated nighttime temperatures support their activity (Mebert et al., 2011; Scali, 2011; Tuniyev et al., 2011; Spaseni et al., 2024).

While numerous studies detail nocturnal aquatic foraging in natricine snakes, they seldom include data on sex, morphological traits or reproductive condition, leaving it unclear whether specific individual characteristics are correlated with nocturnal activity (Mebert et al., 2011; Scali, 2011; Tuniyev et al., 2011; Spaseni et al., 2024). Additionally, despite possible benefits such as lower heat stress, reduced activity of diurnal predators and decreased desiccation risk, nocturnal foraging could instead present significant costs such as reduced feeding opportunities and higher metabolic demands (Carothers & Jakšić, 1984; Metcalfe et al., 1998; Kronfeld-Schor et al., 2003; Fraser et al., 2004; van der Vinne et al., 2015). This suggests that the adaptive value of nocturnal foraging likely emerges only when particular environmental and physiological conditions coincide. These advantages may be further enhanced when nocturnal foraging is temporally aligned with predictable peaks in prey availability, thereby facilitating prey capture. Because most natricine snakes consume amphibians and fish, which themselves exhibit marked seasonal pulses in activity, it is plausible that certain aspects of nocturnal foraging are synchronised with these periodic resource peaks.

In this study, we report repeated, previously undocumented large-scale nocturnal feeding events in two semi-aquatic natricine snake species – the dice snake *Natrix tessellata* and the Balkan grass snake *Natrix natrix persa* - occurring on the shores of Lake Prespa. These feeding events appear to be temporally synchronised with the seasonal spawning of an endemic fish, the Prespa bleak *Alburnus belvica*.

Natrix tessellata and *N. natrix persa* may occur in sympatry but differ markedly in habitat use and trophic ecology. The former is strongly aquatic and primarily piscivorous, whereas the latter is more terrestrial and exhibits a broader diet that includes amphibians, fish and invertebrates (Janev Hutinec &

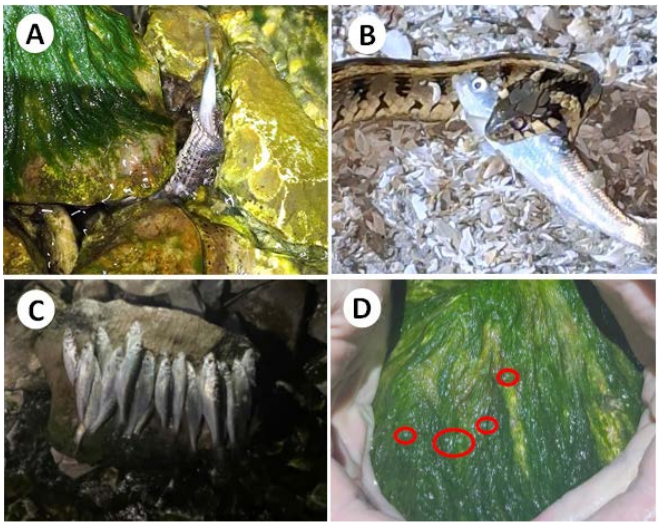

Figure 1. A. A dice snake feeding during the spawning event on Golem Grad, **B.** A Balkan grass snake feeding during the spawning event in Konjsko, **C.** Regurgitated fish from the snakes captured on Golem Grad, **D.** Fish eggs deposited in the shallow waters on the beach, circled in red

Mebert, 2011; Šukalo et al., 2014). Where they coexist, both species can attain high local population densities (Speybroeck et al., 2016). In this study, dice snakes were sampled on Golem Grad Island (40° 52'08" N, 20° 59'23" E) and in the nearby village of Konjsko (40° 54'42" N, 20° 59'26" E), whereas Balkan grass snakes were sampled only in Konjsko due to their absence from Golem Grad. Both sites lie on the shores of Lake Prespa, in Galičica National Park, North Macedonia. Golem Grad (~18 ha), characterised by rocky shorelines and stands of Greek juniper, is locally known as 'Snake Island' because of its historically dense dice snake population (Ajtić et al., 2013). Konjsko, an old fishing village with pebble beaches, reed and willow patches, and an inland oak-meadow mosaic, supports populations of both snake species (Bjelica et al., 2022).

During field surveys on the shores of Golem Grad in August 2023 and July 2024, dice snakes were observed swimming near the shoreline and remaining submerged for extended periods between 21:00–23:00 h. A focused nocturnal survey on 14 July 2024 recorded a pronounced surge in snake activity coinciding with a Prespa bleak spawning event, during which intense fish activity along the shallow, rocky shoreline, characterised by thrashing individuals and the deposition of fish eggs on

Table 1. Summary of nocturnal surveys of *Natrix tessellata* and *Natrix natrix persa* on Golem Grad Island and in Konjsko, showing numbers of captured individuals by sex and reproductive condition

Locality		**Golem Grad**		**Konjsko**
Date		14 July 2024	12 July 2025	8 July 2025
Time		21:00–22:30 h	20:30–22:00 h	20:30–21:35 h
Natrix tessellata	F	23 (SVL 65–101 cm)	24+13PP (SVL 35–97 cm)	4+2PP (SVL 36–81 cm)
	GF	-	7 (SVL 77–102 cm)	-
	M	6 (SVL 52–67 cm)	11 (SVL 51–70 cm)	-
Natrix natrix persa	F	-	-	15+1PP (SVL 45–100 cm)
	GF	-	-	2 (SVL 81–87 cm)
	M	-	-	7 (SVL 58–75 cm)
Tc ◦C		25.5	24.0	22.0
Tw ◦C		24.7	23.5	23.8
Regurgitated fish		N = 24, L = 10.5 ± 1.1 cm, M = 9.7 ± 1.7 g	N = 9, L = 11 ± 0,8 cm, M = 10.6 ± 2.5 g	N = 17, L= 10 ± 1.4 cm, M = 9.8 ± 2.4g

F- non-gravid female, GF - gravid female, PP- post partum female, M - male, SVL- snout-vent length, Tc - cloacal temperature, Tw - water temperature, N- number of regurgitated fish, L - mean body length of regurgitated fish ± sd, M - mean body mass of regurgitated fish ± sd

vegetation-covered rocks, attracted numerous snakes (Fig. 1; BHS video, 2026a; 2026b). Over a 30-minute interval along a five-metre stretch of shoreline, 29 snakes were captured from which a total of 24 regurgitated fish were collected (Table 1), sampling was then suspended to avoid further disturbance. We also recorded the cloacal temperature of captured individuals and the water temperature using a probe thermometer (TP 101). The average cloacal temperature of captured snakes was 25.5 °C and the water temperature was 24.7 °C.

To assess whether these events are regular rather than incidental and occur beyond Golem Grad, additional surveys were conducted at two localities. On 8 July 2025, in Konjsko, both dice snakes *N. tessellata* and Balkan grass snakes *N. natrix persa* were observed feeding on spawning *A. belvica* along the north-western shoreline between 20:30 and 21:35 h, peaking between 20:50 and 21:20 h. Snakes were initially immobile among vegetation, but moved toward the beach and swam along the shoreline as fish activity intensified, with dense schools aggregating around 21:10 h and exhausted fish concentrating in shallow water (Fig. 1; BHS video, 2026c; 2026d). In total, 31 snakes were captured including both dice snakes and Balkan grass snakes from which 17 regurgitated fish were collected (Table 1). The average cloacal temperature of captured snakes was 22 °C, while the water temperature was 23.8 °C.

On 12 July 2025, between 20:30–22:00 h, repeated nocturnal survey on Golem Grad's western beach recorded similar events, with dense spawning aggregations of fish coinciding with intense dice snake foraging. Peak activity occurred between 21:00 and 22:00 h, during which 55 snakes were captured from which 9 regurgitated fish were collected (Table 1). The average cloacal temperature was ~24 °C and water temperature 23.5 °C.

Our nocturnal surveys showed that both dice snakes and Balkan grass snakes actively forage on spawning Prespa bleak in the shallow waters by the shoreline of Lake Prespa. They were made in consecutive years during the same season and included numerous individuals of varying sex and reproductive condition (Table 1). Together, these findings suggest that nocturnal foraging in these natricine snakes is closely linked to a predictable fish spawning event, revealing a previously understudied aspect of their foraging ecology that potentially involved hundreds of snakes. Such synchronised increases in predator foraging in response to seasonally timed prey movements and spawning events are well documented in other taxa, resulting in 'feeding frenzy' behaviour under conditions of exceptionally high prey density (Deacy et al., 2018; Lang et al., 2019; Montero-Quintan et al., 2021).

These results offer new insights into the reproductive biology of natricine snakes. Gravid females are commonly thought to avoid feeding, due to the locomotor and digestive constraints imposed by developing eggs or embryos (Seigel et al., 1987; Brischoux et al., 2011; Brown & Shine, 2025), and most snake species exhibit prolonged fasting during gestation in the wild (Brischoux et al., 2011). Although occasional feeding by gravid females is known, primarily in captivity, it is considered rare in the wild (Brown & Shine, 2025; Brischoux et al., 2011). Our observations of gravid individuals feeding nocturnally (16% of captured female dice snakes and 10% of captured female grass snakes, see Table 1 for details) suggest that these females may exploit brief, high-reward opportunities when ecological conditions are exceptionally favourable. Such events may help offset the substantial energetic demands of reproduction and support post-oviposition recovery (Shine, 1980; Schuett et al., 2013; Bauwens & Claus, 2019). The participation of post-partum females in nocturnal feeding events further indicates that reproductive recovery may be facilitated by these resource pulses. These mechanisms may contribute to maintaining the notably high snake densities documented on Golem Grad (Ajtić et al., 2013).

A final consideration is that our surveys detected mostly adult individuals, with only 10.4% of captured snakes being immature dice snakes (defined as males below 55 cm and females below 63 cm snout-vent length; Ajtić et al., 2013; Table 1). The scarcity of immatures suggests two non-exclusive explanations: (i) immature snakes may not participate in these nocturnal feeding events, possibly due to gape limitations, reduced locomotor capacity or other size-related constraints that limit their foraging opportunities; or (ii) our

sampling protocol may have biased detections by overlooking smaller individuals. Determining whether this pattern reflects true age-specific behavioural differences or methodological limitations is an important avenue for future research on the nocturnal ecology of natricine snakes.

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BHS Video (2026b). Nocturnal feeding by the dice snake (*Natrix tessellata*) while Prespa bleak spawn at Golem Grad. https://youtube.com/shorts/nSVxrYZUEaw.

BHS Video (2026c). Spawning behaviour of the Prespa bleak (*Alburnus belvica*) at Konjsko. https://youtube.com/shorts/ibhFXA54X1M.

BHS Video (2026d). Nocturnal feeding by the Grass snake (*Natrix persa*) during a spawning event of the Prespa bleak (*Alburnus belvica*) at Konjsko. https://youtube.com/shorts/9LO0e0ZsfQw.

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