

Postprandial refuge selection strategy in the Montpellier Snake, *Malpolon monspessulanus* (Hermann, 1804), in a human-altered landscape

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In snakes, ingesting a large meal greatly increases postprandial vulnerability. Reduced mobility, vigilance, and escape efficiency during digestion result partly from morphological and functional constraints associated with body and head shape, as well as feeding performance (Arnold, 1993; Andrade et al., 1997; Secor and Diamond, 1997; Aubret et al., 2007; Hudry and Herrel, 2025). Broad patterns of dietary variation among snake species, including differences in prey size and foraging ecology, can further modulate these constraints (Luiselli, 2006). Movements performed while carrying a large meal increase mortality (Bonnet et al., 1999), prompting individuals to seek a secure and thermally suitable refuge (Webb and Shine, 1998). Foraging strategy can influence extinction risk in reptiles by shaping exposure to predators and energetic trade-offs (Baeckens et al., 2023). In Mediterranean anthropogenic landscapes, suitable natural refuges are often scarce, forcing snakes to rely frequently on artificial structures for shelter (Todd et al., 2010). In this context, we present standardised field observations from seven large adult male Montpellier Snakes, *Malpolon monspessulanus* (Hermann, 1804), tracked in three human-modified areas of southeastern France, focusing on postprandial movement distances to refuges and the characteristics of refuges used during digestion.

We staged feeding events by presenting a dead prey item to snakes that were radio tracked and recorded their feeding behaviour. Firstly, seven adults (920–1650 g; 1500–1880 mm total length) were captured in agricultural and peri-urban landscapes across three study sites (Bédarrides: 44.0352°N, 4.8805°E; Entraigues-sur-la-

Sorgue: 44.0086°N, 4.9069°E; Cavaillon: 43.8202°N, 5.0590°E). These snakes were surgically implanted with intracoelomic radio transmitters VHF (Holohil, model SB-2, 5 g), representing less than 5% of body mass for all individuals, and released shortly thereafter during warm periods to promote rapid wound healing. Feeding events of these seven snakes were conducted opportunistically between June 2021 and July 2024 during the warmer periods of the year, as part of broader studies on the spatial ecology of the Montpellier Snake. The feeding events were recorded using camera traps. The first feeding trials involving the ingestion of large meals were conducted no earlier than four weeks after transmitter implantation, ensuring sufficient recovery time following surgery. All snakes readily consumed the prey, and no abnormal behaviour or disturbance was observed during feeding. All procedures were performed under veterinary supervision following established protocols for transmitter implantation in snakes (Reinert and Cundall, 1982; Hale et al., 2017). This implantation technique has recently been reported as effective for this species under field conditions (del Barrio et al., 2025).

Each snake received one or more euthanised prey items (entire rats or chicken legs) representing 7–36% of its body mass. Ingestion (8–20 min) was confirmed using camera traps (Deso et al., 2022; Deso and Bonnet, 2023). Snakes were radio-tracked immediately after swallowing until they reached the refuge used for digestion. Straight-line postprandial distances were measured with a GPS. Predator accessibility to refuges was assessed considering potential avian and terrestrial mammalian predators, as well as human access in anthropogenic contexts. Refuges were classified as accessible when they could be easily reached or opened by a human hand or accessed by avian and terrestrial predators, moderately accessible when access was limited by narrow entrances, partial cover, or required deliberate manipulation, and inaccessible when physical

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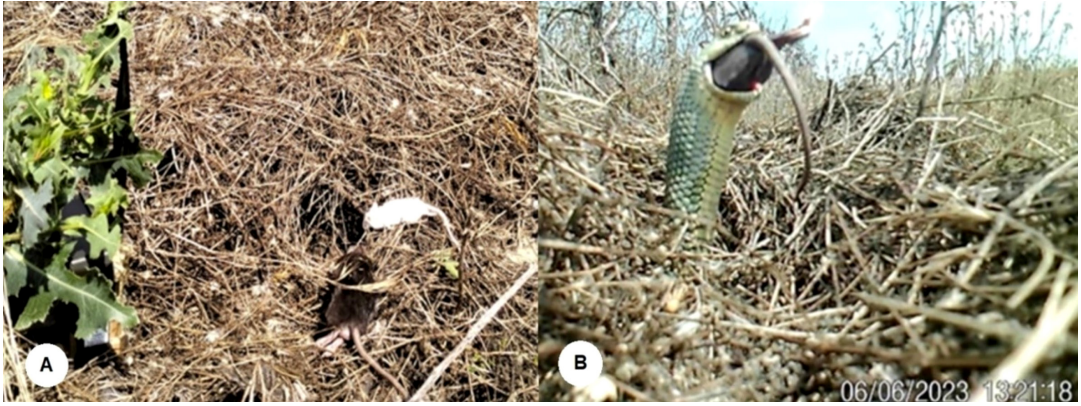


Figure 1. (A) Example of the camera-trap setup showing the placement of the prey item and the camera's field of view; (B) Feeding event recorded by a camera trap: a male Montpellier Snake (*Malpolon monspessulanus*) ingesting a rat.

barriers or deep, narrow structures prevented access by most predators and humans. We used a linear regression to examine the relationship between meal mass and postprandial distance; and a multinomial logistic regression to summarise the influence of refuge type.

A total of 18 feeding events were recorded across seven adult individuals, with one to five events per snake. For individuals monitored more than once, consecutive feeding events were separated by several weeks to several months. These events led to the identification of 14 digestive refuges, most of which are illustrated in the associated video material available at <https://doi.org/10.5281/zenodo.18001666>. Postprandial distances ranged between 2–171 m. Light meals were associated with short movements (< 30 m), whereas the heaviest meals produced movements > 100 m. Distance increased strongly with meal mass ($R^2 = 0.81$, $p < 0.001$). Among the 14 refuges, 61% were anthropogenic and 39% natural. Natural refuges were almost always accessible to predators, whereas anthropogenic refuges were mostly moderately accessible or inaccessible to predators, with the likelihood of using a difficult-to-access refuge increasing with meal size.

Although our sample size remains limited (seven individuals tested), our results suggest that large meals tend to increase the distance required to reach a secure shelter, thereby amplifying postprandial vulnerability (Cruz-Neto et al., 1999; Bonnet et al., 2001; Crotty and Jayne, 2015). Refuge selection and postprandial movements in free-ranging snakes are influenced by multiple interacting ecological and individual factors that are difficult to fully control under natural conditions. In addition to meal size, refuge availability

and accessibility within the surrounding landscape likely constrain the set of shelters effectively available to an individual. Vegetation structure and habitat characteristics at and around the feeding location may further influence movement paths and refuge choice. Short-term environmental conditions, such as weather, may also affect postprandial behaviour, although these variables could not be explicitly incorporated into the present analyses. Larger snakes are often assumed to tolerate longer movements to reach secure shelters, which could influence postprandial distances independently of meal size. However, previous studies have reported no significant sex-related differences in home range size in *M. monspessulanus* (females being markedly smaller in this species; see Monrós, 1997), and our study focused exclusively on large adult males, thereby preventing any assessment of the respective effects of body size and sex. Given the uneven distribution of feeding events among individuals and the limited sample size, the influence of individual characteristics (such as behavioural tendencies or personality-related traits, Skinner et al., 2022) should be considered when interpreting the observed relationships between meal size, postprandial movement distance, and refuge characteristics. The apparent gap in postprandial movement distances between approximately 55 and 100 m likely reflects the combined effects of meal size and individual-level variation rather than a discrete behavioural threshold. In our dataset, short movements were consistently associated with lighter meals, whereas long movements occurred only after the ingestion of large prey, suggesting a non-linear response to meal mass. Additionally, repeated feeding events for

some individuals raise the possibility that individual tendencies or spatial familiarity may contribute to clustering of movement distances. However, the limited sample size and uneven replication precluded the use of multivariate or mixed-effects models incorporating individual identity and body size as random factors. As such, the observed distribution should be interpreted cautiously and viewed as an emerging pattern that warrants further investigation with larger sample sizes.

This pattern aligns with optimal digestive strategy models predicting higher costs associated with large meals in infrequently feeding snakes (Wood and Ruxton, 2025). These first standardised field observations on large adult Montpellier Snakes highlight the need for further research on the biomechanical and ecological constraints associated with heavy meals in this species. In anthropogenic landscapes, artificial structures can occasionally provide refuges that are more protective than natural shelters, but their stability is strongly dependent on ongoing human activities (Todd et al., 2010). Such reliance on unstable shelters may contribute to the observed sensitivity of large individuals in Mediterranean populations (López-Calderón et al., 2017), a pattern with potentially important demographic consequences given the central role of adult survival and reproductive output in snake population viability (Shine and Bonnet, 2009). Preserving stable, deep, and narrow refuges (whether natural or artificial) appears essential to reduce postprandial exposure and associated risks. In peri-urban and intensively farmed landscapes, stable artificial shelters associated with thermally favourable micro-sites may help reduce risky postprandial movements following the ingestion of large meals, a hypothesis that warrants further evaluation in land-use planning contexts alongside existing natural refuges.

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References

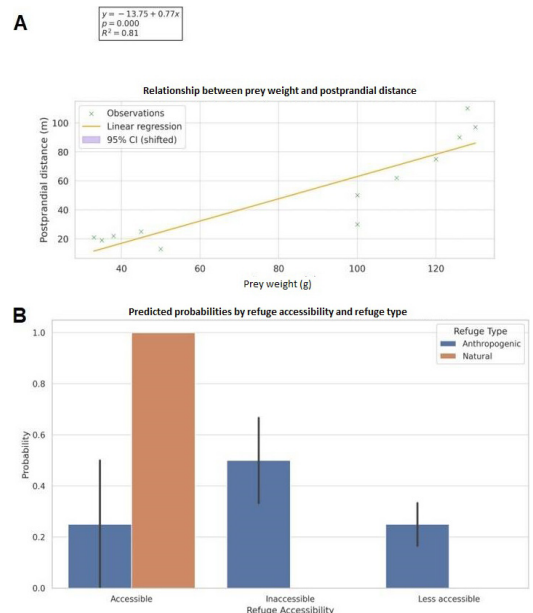


Figure 2. (A) Relationship between prey weight and postprandial straight-line distance in seven adult Montpellier Snakes ($n = 18$). (B) Predicted probabilities of refuge-accessibility categories (accessible, moderately accessible, inaccessible) according to refuge type (anthropogenic vs. natural) and prey-weight class.

- Andrade, D.V., Cruz-Neto, A.P., Abe, A.S. (1997): Meal size and specific dynamic action in the rattlesnake *Crotalus durissus*. *Herpetologica* **53**: 485–493.
- Arnold, S.J. (1993): Foraging theory and prey-size–predator-size relations in snakes. In: Seigel, R.A., Collins, J.T. (eds.): *Snakes: Ecology and Behavior*. McGraw-Hill, New York: 87–115.
- Aubret, F., Bonnet, X., Bradshaw, D. (2007): Food versus risk: foraging decision in juvenile tiger snakes *Notechis scutatus*. *Amphibia-Reptilia* **28**: 304–308.
- Baeckens, S., Meiri, S., Shine, R. (2023): Foraging mode affects extinction risk in reptiles, but in different ways. *Conservation Letters* **16**: e12977.
- Bonnet, X., Naulleau, G., Shine, R. (1999): The dangers of leaving home: dispersal and mortality in snakes. *Biological Conservation* **89**: 39–50.
- Bonnet, X., Naulleau, G., Shine, R., Lourdaix, O. (2001): Short-term versus long-term effects of food intake on reproductive output in a viviparous snake (*Vipera aspis*). *Oikos* **92**: 297–308.
- Crotty, T.L., Jayne, B.C. (2015): Trade-offs between eating and moving: what happens after a big meal in arboreal snakes? *Biological Journal of the Linnean Society* **114**: 446–458.
- Cruz-Neto, A.P., Andrade, D.V., Abe, A.S. (1999): Energetic cost of predation: aerobic metabolism during prey ingestion by juvenile rattlesnakes (*Crotalus durissus*). *Journal of Herpetology* **33**: 229–234.
- del Barrio, G., Laurence, F., Deso, G., Cuvelier, J., Bonnet, X.

- (2025): Pose interne d'émetteurs pour le radio-tracking chez deux espèces de serpents du sud de la France. *L'Essentiel Vétérinaire*. 781/782: 29–32.
- Deso, G., Crouzet, A., Bonnet, X. (2022): Food supplementation of the Montpellier snake *Malpolon monspessulanus* in the wild. *The Herpetological Bulletin* **160**: 23–24.
- Deso, G., Bonnet, X. (2023): Consumption of putrescent carrion by a free-ranging Montpellier snake *Malpolon monspessulanus*. *The Herpetological Bulletin* **165**: 45.
- Hale, A.M., Swearer, S.E., Franklin, C.E. (2017): Surgical implantation of radio transmitters in snakes: safety and outcomes. *Journal of Wildlife Management* **81**: 189–195.
- Hudry, L., Herrel, A. (2025): Divergent paths, convergent heads: morphological adaptation of head shape to Habitat Use and Diet in Snakes. *Journal of Morphology* **286**(11): 1–14.
- López-Calderón, C., Feriche, M., Alaminos, E., Pleguezuelos, J.M. (2017): Loss of largest and oldest individuals of the Montpellier snake correlates with recent warming. *Current Zoology* **63**: 607–613.
- Luiselli, L. (2006): Broad geographic, taxonomic and ecological patterns of interpopulation variation in the dietary habits of snakes. *Web Ecology* **6**: 2–16.
- Monrós, J. (1997): El dominio vital y algunos aspectos de la ecología de la culebra bastarda *Malpolon monspessulanus* en los naranjales. Tes. Doc. Univ, Valencia, 123 pp.
- Reinert, R.A., Cundall, D. (1982): An improved surgical implantation method for radio-tracking snakes. *Copeia* **1982**(3): 702–705.
- Secor, S.M., Diamond, J. (1997): Effects of meal size on postprandial responses in juvenile Burmese pythons. *American Journal of Physiology* **272**: R902–R912.
- Skinner, M., Brown, S., Kumpan, L.T., Miller, N. (2022): Snake personality: Differential effects of development and social experience. *Behavioral Ecology and Sociobiology* **76**: 135.
- Shine, R., Bonnet, X. (2009): Reproductive biology and population viability. In: Mullin, S.J., Seigel, R.A. (eds): *Snakes: Ecology and Conservation*. Cornell University Press, Ithaca: 172–200.
- Todd, B.D., Willson, J.D., Gibbons, J.W. (2010): The global status of reptiles and causes of their decline. In: *Ecophysiology of Amphibians and Reptiles*. CRC Press, Boca Raton: 47–67.
- Webb, J.K., Shine, R. (1998): Thermoregulation by a Nocturnal Elapid Snake (*Hoplocephalus bungaroides*) in Southeastern Australia. *Physiological Zoology* **71**: 680–692.
- Wood, J.E., Ruxton, G.D. (2025): A model of optimal digestive strategy in infrequently-feeding snakes. *Evolutionary Ecology* **39**: 37–56.