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What can the location of skin sheds tell us? A case study on Montpellier snake *Malpolon monspessulanus* in southeast France

Marc Cheylan[1,*], David Stubbs[2], Pauline Priol[3]

[1] Ecole Pratique des Hautes Etudes, Université Paris Sciences Lettres, 4-14 rue Ferrus, Paris, France.
[2] Sustainability Experts Ltd., Sterling House, Hatchlands Road, Redhill, Surrey RH1 6RW, UK.
[3] Statipop, scientific consulting, Cazilhac, France.

*Correspondence: marc.cheylan@mail.com

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Montpellier snake *Malpolon monspessulanus* (Hermann, 1804) skin sheds were collected over four years from an olive grove (0.21 ha) in southeast France. Examination of the cephalic scales allowed us to identify the individuals that frequented the site and the regularity of their visits for shedding. Reconstruction of the life histories of the individuals by capture-mark-recapture modelling showed that they visited the site during four consecutive years to shed. This site fidelity could be linked to mating opportunities or egg laying and foraging, or to the distinctive nature of the site, which is a sunny clearing within a dense woodland not very suitable for this thermophilic species. The concentration of the population in a very small area at certain times of the year risks making it vulnerable to predators as well as to changes that the site may undergo in the future, particularly if its agricultural use is abandoned and the woodland encroaches the open field area.

Key words: Montpellier snake; site fidelity; sloughing; southern France.

In snakes, the shedding process is an important phase in the animal's life that results in significant physiological and behavioural changes. A few days before moulting, the eyes become cloudy, the skin discolours, thermal needs increase and the snake becomes more aggressive. The moult sheds in one piece, generally from the rostral scale. The snake frees itself quickly from the old skin by virtue of a fatty liquid that facilitates its peeling off. This renewal of the skin occurs several times a year, generally two to three times during the snake's activity season in temperate regions. The Montpellier snake *Malpolon monspessulanus* (Hermann, 1804) is a singular species among European snakes as it belongs to an essentially African family, the Psammophiidae, which gives it several original characteristics: an opisthoglyphous envenomation system, a vernal rather than summer sexual cycle (CHEYLAN *et al.*, 1981; FERICHE *et al.*, 2008), and a self-rubbing behaviour unique among snakes (DE HAAN, 2003; DE HAAN & CLUCHIER, 2006). This behaviour consists of rubbing the entire body with the nasal region, where the glands secrete an oily liquid that the animal spreads on the skin by vertical movements of the head. This behaviour is used to chemically mark the substrate or conspecific individuals, as has

DOI: http://dx.doi.org/10.11160/bah.264 Supplementary material available online been shown by DE HAAN (2003).

Although this species has been fairly well studied in the wild and in captivity (BLAZQUEZ, 1995; DE HAAN, 1999; PLEGUEZUELOS, 2021), several aspects of its ecology remain unknown. The collection of skin sheds deposited over several years on a site located in a woodland clearing in the south of France has provided unexpected new information on the fidelity of the species to a given location and on the probable interactions between individuals. This study discusses how the regular collection of sloughed skins revealed little-known aspects of the ecology of this species, such as site fidelity and adult survival rates.

MATERIALS AND METHODS

Study site and sample collection

The study site was an olive grove of about 2170 m^2, located west of the village of Les Mayons in southeast France (43.309° N, 6.354° S). This olive grove consists of four earthen terraces supported by dry stone walls about 1.30 m high, known locally as *restanques*. The surrounding area is covered by dense woodland, consisting mainly of old cork oaks (*Quercus suber*) and chestnut trees (*Castanea sativa*), with an undergrowth dominated by strawberry trees (*Arbutus unedo*) and tree heather (*Erica arborea*) (Fig. 1). The climate is humid Mediterranean, with an average minimum temperature of 8.4°C and an average maximum of 20.4°C, and an average annual rainfall of 890 mm (measurements from the Luc-en-Provence station, located 9 km from the site) (KESSLER & CHAMBRAUD, 1986).

The skin sheds were collected during a separate study of the ecology of the Hermann's tortoise *Testudo hermanni* (STUBBS & SWINGLAND, 1985), which also lives in this habitat, throughout the months the tortoise is active (March to end of October). In 1981, Adrian Hailey collected 17 adult skin sheds from the site (HAILEY, 1982); unfortunately, these were not preserved and are therefore not included in this study. That same year we collected two adult skin sheds from the site. In 1982 and 1983, the visits to look for skin sheds were made more regularly, with four or five visits per week from February to October in 1982 (except for some weeks in July-August) and from March to September in 1983 (except for some weeks in late April-early May). In 1984, only two visits to collect

Figure 1: The study site in 1983 (author: David Stubbs)

Table 1: Number of *Malpolon monspessulanus* skin sheds found at the study site and number of different individuals identified per year, including number of visits during which skin sheds were found (Visits), total number of collected skin sheds (Sheds), and number of different individuals to which the collected sheds belonged (Individuals).

Year	Visits	Sheds	Individuals
1981	?	19	2*
1982	6	19	16
1983	4	12	12
1984	2	13	11
Total	13	46	26

skin sheds were made to the site, one in July and the other in August (Table 1).

After being collected in the field, the sloughed skin was moistened so that it could be turned inside out (external side up) and then glued to card, noting date, snout-vent length and tail length where possible. They were then covered with a transparent film and stored away from light and moisture.

Due to the small number of collected skin sheds (N = 46), individuals were identified by sight, based on the scales bordering the parietal plates. This method has been used for the specific (TSAI & MAO, 2017) and individual identification of snakes (GRAY, 2008), particularly European vipers, which show high variability in the scales on the top of the head (BENSON, 1999; STOYANOV & TZANKOV, 2017). In the Montpellier snake, scale variability mainly occurs around the parietal plates, as shown in Figures 2 and 3. To facilitate the identification of individuals, skin sheds with the same number of scales bordering the right parietal plate were separated into three batches, and when two skin sheds had the same scale pattern, identification was confirmed on all cephalic scales. A blind test by two different observers produced the same results, validating the reliability of the method for this species.

Statistical analysis

The identification of skin sheds made it possible to construct a capture-mark-recapture (CMR) matrix with the individuals in rows and the years of collection of skin shed in columns (Table S1).

The data were modelled using Pradel's survival and seniority models. These models allow simultaneous estimations of survival and recruitment (1 - seniority) while taking into account varying capture probability (PRADEL, 1996; PRADEL *et al.*, 2009). To

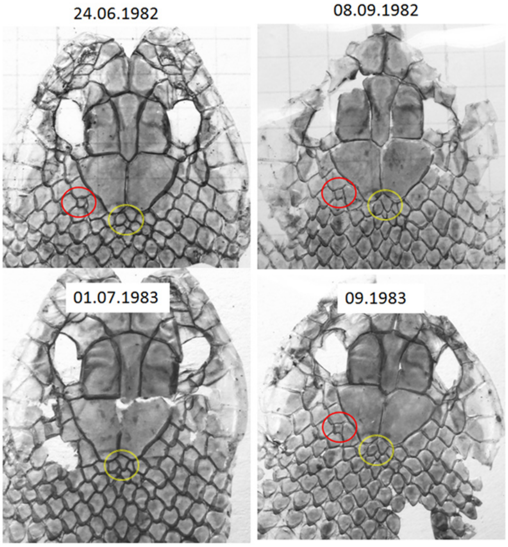

Figure 2: Individual number 8, identified in four skin sheds found in 1982 and 1983. The circles indicate the characteristic scales of this individual.

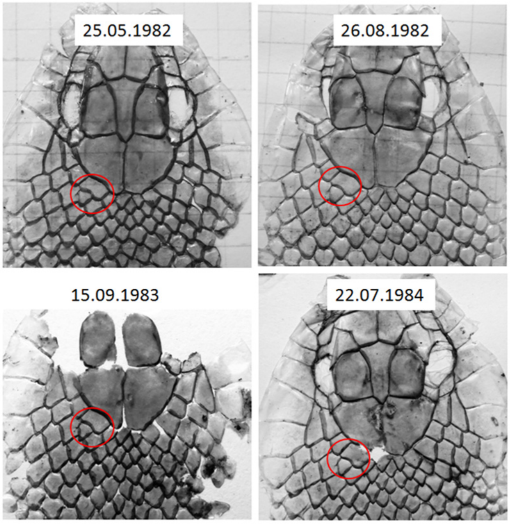

Figure 3: Individual number 7, identified in four skin sheds found in 1982, 1983 and 1984. The circles indicate the characteristic scales of this individual.

permit the models to converge and provide outputs, the capture (first time a shed was collected) and recapture probabilities were considered equivalent. We compared models in which parameters (survival, recruitment, capture probability) were constant (referred to as '.') or varied from year to year (referred to as 'year'). This resulted in a set of eight models that were fitted using MARK 6.2 (WHITE & BURNHAM, 1999). The models were compared using the Akaike information criterion adjusted for small sample sizes (AICc) (BURNHAM & ANDERSON, 2002). All estimations are provided with 95% confidence intervals.

RESULTS

Chronology of skin sheds

The earliest skin sheds found in an activity season were on 21 May in 1982 and 25 May in 1983, and the latest found was on 10 October in 1982. The skin sheds were found with maximum frequency in June (N = 9), September (N = 9) and May (N = 7) and with the lowest frequencies in July (N = 2), August (N = 1) and October (N = 1). There were three cases of two sheds belonging to the same individual during one active season: one in May and August, one in June and September, and one in July and September. This indicates at least two sheds per year, spaced 39, 75 and 90 days apart.

Population estimate and site fidelity

Of the 46 capture-recaptures (represented by skin sheds) over the four years of monitoring, we identified 26 different adult individuals. By year, there were 16 different adult individuals in 1982, 12 in 1983 and 11 in 1984 (Table 1).

In the demographic modelling, two models had the most support: both had a combined AICc weight of 0.62 (Table 2). These models considered that capture probability was stable over time, estimated at 0.10 (95% CI: 0.07-0.15); that recruitment (1 - seniority) depended on the year, estimated at 0 between 1981 and 1982 and 0.40 (95% CI: 0.14-0.63) between 1983 and 1984; and that survival was constant or depended on the year, estimated for the two models at 1 (95% CI: 0.99-1).

The models estimated the population size to be 30 individuals (95% CI: 22-52 individuals) in 1982, 29 individuals (95% CI: 19-54) in 1983, and 57 individuals (95% CI: 32-114) in 1984.

DISCUSSION

The Montpellier snake skin sheds collected at the site near Les Mayons provide some insight into the biology of the spe-

Table 2: Description of constraints, Akaike information criterion (AICc), change in AICc (ΔAICc), Akaike weights (AICc weight) and number of estimated parameters (Np) for the eight models obtained from capture-recaptures of skin sheds of *Malpolon monspessulanus* (1982-1984). Model parameters include the survival probability (φ), the seniority probability (G), the probabilities of capture (p) and recapture (c) and the number of missed animals (Fo).

Model	AICc	ΔAICc	AICc weight	Np
φ (.) G(year) p=c(.) Fo(year)	127.89	0.00	0.31	5
φ (year) G(year) p=c(.) Fo(year)	127.89	0.00	0.31	5
φ (year) G(.) p=c(year) Fo(year)	130.23	2.35	0.10	6
φ (.) G(.) p=c(.) Fo(year)	130.30	2.42	0.09	5
φ (year) G(.) p=c(.) Fo(year)	130.30	2.42	0.09	5
φ (year) G(year) p=c(year) Fo(year)	132.45	4.57	0.03	7
φ (.) G(year) p=c(year) Fo(year)	132.45	4.57	0.03	7
φ (.) G(.) p=c(year) Fo(year)	133.13	5.24	0.02	7

cies, but also into the value of collecting snake skin sheds in the wild.

In terms of phenology, the chronology shows that shedding takes place throughout the warm period, reaching a maximum level in May, June and September. However, this chronology is imprecise due to the fact that in certain years, certain periods were not well surveyed: this was the case in July and August 1982 and late April and early May 1983. Field observations indicate that skin sheds were often found on the same day, suggesting some synchronization of shedding or synchronization of site visits by the snakes. Shedding frequency for the same individual was difficult to determine, but the results allowed us to conclude that a snake could sloughed at least twice per activity season, spaced 39 to 90 days apart. In the south of France, DE HAAN (1999) found four to six sheds in captivity in males of this species and three to five in females between May and October, which corresponds to the dates observed at the Les Mayons site. In southern Spain, BLÁZQUEZ (1993) and MILLÁN (1994) located adult sheds earlier in the year, mainly between March and June. Based on these findings, the number of skin sheds found at our site and the number of identified individuals suggest that only some sheds took place in the olive grove.

In terms of demography, the study made it possible to estimate population size and site fidelity. The identification of individuals suggested a strong attachment to the site in adults, a fidelity that extended over at least three years if the most frequently observed skin sheds are taken into account. This site fidelity resulted in the estimation of a survival rate very close to 1, which means that the animals not only survived along the three years of monitoring, but also returned to the site regularly. In Pennsylvania, GRAY (2008) also observed site fidelity for moulting in the species *Storeria dekayi dekayi*.

Recruitment estimates were variable

over time, indicating few new entries between 1982 and 1983 and 40% of new individuals between 1983 and 1984. These results may be due to sampling heterogeneity or could be due to more visits to the site by snakes with a nearby home range, indicating better breeding conditions or better food availability. This site fidelity is also likely explained by the nature of the site: a sunny enclave in the middle of a dense woodland that is not very favourable to insolation or egg laying. It is possible that the gathering of around 30 adult individuals in this olive grove is largely related to reproduction, whether to facilitate encounters between the sexes or suitability for egg laying. Several authors have observed cases of multiple females using the same location for their clutches in this species (BLÁZQUEZ & VILLAFUERTE, 1990; GALÁN & FERNÁNDEZ-ARIAS, 1993; MILLÁN, 1994), giving credence to the idea that cavities at the base of dry-stone walls or at the foot of olive trees may be good conditions for incubating eggs. It is also possible that the thermal conditions offered by this olive grove are attractive for individuals in their ecdysis phase, due to greater thermal needs during this period (DUPOUÉ *et al.*, 2015). An examination of aerial photos shows that there are no similar areas in a radius of 250 m, which approximately represents the range of action of a Montpellier snake (between 3.27 and 5.48 ha, according to MONRÓS, 1997).

The population estimate obtained by modelling data from the two best monitored years (30 individuals in 1982 and 29 in 1983) was in line with the count of the number of different individuals obtained for the period 1982-1984 (24 individuals). Given the small size of the site (0.2 ha), it is clear that these approximately 30 individuals did not occupy the site all year round. They are likely to occur there occasionally, during certain stages of their life cycles like shedding, mating, or egg laying. The home range for this species assessed in Spain by MONRÓS (1997) ranges from 3.27 ha for females to 6.48 ha for males, i.e. values 16 to 32 times greater than the site where the skin sheds were collected. This lends credence to the idea that the olive grove is a gathering site for the population. This aggregation implies a certain tolerance between individuals, although males are known to mark their territory with their nasal secretions and to protect favoured females (DE HAAN, 1999; DE HAAN *et al.*, 2006; BONNET *et al.*, 2022). Observations in the wild as well as in captivity show that male Montpellier snakes cam cohabit peacefully, as long as the established behavioural rules between dominant and subordinate males are respected (DE HAAN, 1999). The information obtained in our study is therefore consistent with peaceful cohabitation during key active periods of the species.

The aggregation of the entire adult population also raises interesting questions for the conservation of the species. It makes the population doubly vulnerable: to predators and to changes occurring at the site where they gather. A parallelism can be drawn with studies carried out on the Hermann's tortoise population occupying the site (STUBBS & SWINGLAND, 1985; SWINGLAND & STUBBS, 1985), which showed that the concentration of egg laying in this olive grove resulted in a very high predation rate of the eggs, which could reach

Figure 4: Evolution in woodland cover between 1958 and 2000 (IGN images). The olive grove where the present study was conducted is indicated.

95% in the days following their laying (SWINGLAND & STUBBS, 1985). This observation was later confirmed experimentally by MADEC (1999), when artificial nests reproducing Hermann's tortoise eggs were installed in the same olive grove. Demographic monitoring of Hermann's tortoises showed a population collapse of nearly 73% between 1983 and 1999, largely explained by the change in woodland cover surrounding the olive grove and the intensity of predation on eggs and individuals (COUTURIER *et al.*, 2014). During the period 1950-2008, dense woodland surrounding the site increased considerably, covering the site from 32% in 1950 to 70% in 2008

(TILLION, 2011), therefore, reducing the area of open landscape suitable for Mediterranean reptiles (Fig. 4). Unfortunately, there is no availability of aerial pictures of the site during the years when the study was conducted.

It is possible that the causes of decline cited for the Hermann's tortoise population are also true for the Montpellier snake population, a hypothesis that could be confirmed by revisiting the site in the coming years. The maintenance of this olive grove, and of the few open areas still present in the sector, seems in any case necessary for the local survival of these two species. Overall, these findings show that the reduction and fragmentation of favourable habitats often lead to negative demographic dynamics, which can endanger the future of many animal populations (FAHRIG, 2003; NEWBOLD *et al.*, 2015; FARDILA *et al.*, 2017).

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