Long-term fidelity to communal oviposition sites in *Hierophis viridiflavus*

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A communal oviposition site of western whip snakes, *Hierophis viridiflavus*, was surveyed every June for 13 years (1990–1997; 2001–2005) at a hilly locality of central Italy (Oriolo Romano, province of Viterbo, about 400 m a.s.l.). The snakes were individually marked, and hence the individual histories of several specimens were assessed over more than one year. The oviposition site was a partially dilapidated building with stony boxes, surrounded by spiny shrubs. Overall, at the study site, 41 gravid females were captured over 13 years of study, together with five adult males and 189 newborn snakes. No non-gravid females were found. Hence, it seems that the study site is used by snakes solely for egg-laying. In total, 73 oviposition events occurred in the study area, and on average the study area was visited annually by 5.46±1.05 gravid females (range 4–7). Gravid females visited the study area for periods of 2.20±1.38 years (range 1–5 years); some individuals visited the study site in consecutive (up to three) years, others in alternate (up to five) years, and others at irregular intervals (up to four years). The communal oviposition site was not used preferentially by any specific size category of snakes, but every gravid female in the population, from those presumably young (around 110 cm in length or less) to those presumably old (longer than 120 cm) appeared to use it regularly for laying eggs. There was an effect of year on snake clutch size, but not on the mean body size of snakes. The criteria used by snakes for the selection of the study area as an oviposition site were 1) safe conditions, due to a scarcity of natural predators, and 2) adequate conditions for egg development in a area with resource scarcity for adequate oviposition sites for snakes.

Key words: Colubridae, Italy, Mediterranean habitat, reproductive biology, Reptilia, Squamata

INTRODUCTION

Maximizing offspring survival is one of the main priorities for any responsible mother in the animal world (e.g. Roff, 1992). In oviparous snakes, egg development is temperature-dependent and depends largely on the "quality" of the environment where the eggs are laid (Ackerman & Lott, 2004; Birchard, 2004); hence one of the main priorities for female snakes is to find good oviposition sites with optimal thermal, hydric and respiratory conditions where the eggs can be optimally incubated and that are relatively inaccessible to predators (Ackerman & Lott, 2004; Birchard, 2004). When good oviposition sites are a limited resource, the female snakes might be expected to find strategies that maximize egg survival. The most obvious strategy for females is to travel rapidly over long distances to find good oviposition sites (e.g. Madsen, 1984a,b, 1985), sometimes selecting habitats that are thermally warmer, less variable (e.g. Reinert, 1984), or wetter (Shine, 1979). However, other less obvious strategies may be used. For instance, the females of the Afrotropical water snake *Grayia smythii* resist the dry season constraints and the abundance of egg predators by depositing their eggs in more than one oviposition site rather than laying at a single site (Akani & Luiselli, 2001). Thus, these snakes exhibit an oviposition strategy resembling that of several chelonian species (e.g. Zuffi & Odetti, 1998). On the other hand, other snakes use exactly the opposite strategy, i.e. several females join together to deposit all their clutches inside a communal oviposition site. Communal oviposition sites have been observed in several snake species (e.g. Fitch, 1958; Gordon & Cook, 1980; Plummer, 1981; Rasmussen, 1993; Albuquerque & Ferrarezzi, 2004; James & Henderson, 2004), including the European species *Natrix natrix* (Matheson, 1962; Kabisch, 1974; Lapini, 1983), *Zamenis longissimus* (formerly *Elaphe longissima*) (Lapini, 1983; Gomille, 2002), and *Hierophis viridiflavus* (formerly *Coluber viridiflavus*) (Capula & Luiselli, 1995).

However, although the occurrence of communal oviposition behaviour is well-known in the reproductive biology of snakes, almost nothing is known regarding the ecology of this behavioural pattern. Capula & Luiselli (1995) studied this phenomenon in the western whip snake, *H. viridiflavus*, during three consecutive years (1990–1992) at a locality in central Italy, and observed that some females visited the same communal oviposition site for more than one year.

In this paper, by using the same study system as that of Capula & Luiselli (1995) – i.e. the same population of *H. viridiflavus* at the same communal oviposition site – but

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studied longitudinally for a much longer timespan (13 years), we address the following questions:

1) Are communal oviposition sites used for prolonged periods by a given snake population?

2) If yes, is individual site fidelity or individual turnover high between years?

3) How many females (on average) use the communal oviposition site?

4) Are communal oviposition sites used by a particular size category of females or more generally by females of any size?

5) Are there yearly differences in the body size and clutch size of the females using the communal oviposition site?

6) What criteria are used by gravid female snakes in their selection of communal oviposition sites?

MATERIALS AND METHODS

Study area

The field study was conducted at Oriolo Romano (Province of Viterbo, about 400 m a.s.l.), 60 km north of Rome. The site was characterized by a partially dilapidated building (a stony box measuring 5.0 x 3.5 m, height 5 m) bordered by rich spiny vegetation (mainly *Rubus* sp.) and completely surrounded by cultivated fields. The climate of the study area is Mediterranean temperate, with hot, dry summers, cool, wet winters and mild, wet springs and autumns (Tomaselli et al., 1973).

The herpetofauna of the study region (area of Canale Monterano, Tolfa mountains) is well known because of long-term studies on snake ecology that have been carried out in this region (e.g. Capula et al., 1995, 1997; Filippi, 1995; Filippi & Luiselli, 2006; Luiselli & Filippi, 2006).

Hierophis viridiflavus is the only snake species that regularly inhabits cultivated and suburban areas (for instance, at Canale Monterano, see Filippi & Luiselli, 2006; Luiselli & Filippi, 2006). Whip snakes are active at the study area between early March and early November (Capula et al., 1997). Mating occurs from mid-March to the end of April, ovulation takes place at the beginning of June, and oviposition from late June to mid-July (Capula et al., 1995). About 77% of the adult females reproduce every year (Capula et al., 1995), and, on average, each female lays 3–7 eggs (Capula & Luiselli, 1995).

Protocol

The study area was surveyed each year between 10 and 30 June and all whip snakes found during this period were captured. Each year, at least 12 days were spent in the field (each field-day lasting from 0800 to 1800). Additional snakes were captured during regular surveys (about 10 field-days per year) conducted from March to May and from August to November. Each field survey was done by two or three people who searched intensively for snakes throughout the study area. Since the study area was small (i.e. the dilapidated building plus a boundary area of about 100 x 80 m), we are confident that we have encountered most of the whip snakes active in the study area during the survey periods.

Snakes were captured by hand. Once captured, snakes were individually marked by ventral scale clipping for future identification, and if female they were palpated in the abdomen to verify their eventual pregnancy status and the number of eggs. Although we generally used abdominal palpation to determine the number of eggs, in some years (1990–1992) we used radiography. Several studies by ourselves (based on comparison of the egg numbers of the same females as detected by radiography, abdominal palpation and counts of eggs deposited in terrarium) indicated that the precision of the counts by abdominal palpation was accurate to ±1 egg with this snake species (Filippi et al., unpublished data).

Total length (TL, i.e. snout–vent length + tail, in cm) was recorded from each captured snake to the nearest cm.

Statistical analyses

Statistical analyses were done with Statistica 6.4 and SPSS 8.0 for Windows PC packages, with all tests being two-tailed and alpha set at 5%. Means are presented ±1 SD. Linear regression between female length (independent variable) and number of eggs (dependent variable) was assessed by Pearson's correlation coefficient (Zar, 1984), and the data were entered once for each individual snake in order to avoid pseudoreplication (Hurlbert, 1984). For homogeneity, we used only data relative to the first time a given snake was examined.

RESULTS

Overall, 41 gravid females were captured in June during the 13 years of study (Table 1). During the same period, five adult males and no non-gravid adult females were captured. In August–September of the same years, a total of 189 newborn snakes were also captured. The adult female-biased sex ratio (8.2:1, $P < 0.01$ with binomial test), the total absence of non-gravid females and the high abundance of newborn snakes in the sample clearly demonstrated that the study area was used as an egg-laying site by whip snakes.

In total, 73 oviposition events occurred at the study site, including both those of females that oviposited once and more than once (assuming that every gravid female captured in each year successfully produced eggs) (Table 1). On average, the study site was visited annually by 5.46±1.05 gravid females (n=13, range 4–7). Excluding two females that were captured for the first time in the last year of both observation periods (i.e. 1997 and 2005) and that had no possibility of being recaptured later, of the remaining 39 females, 46.1% were found at the study area during only one year, 30.8% in two different years, and 23.1% in three different years (Table 1). Overall, gravid females visited the study area for an average of 2.20±1.38 years (range 1–5), taking into consideration the year of first appearance and the year of last appearance in our samples (Table 1).

Of the females that visited the study area twice (n=12), 58.3% did so in consecutive years, 25% in alternate years, and 16.7% every three or more years (Table 1). Of the females that visited the study area in three different years

Table 1. Gravid *Hierophis viridiflavus* captured during June 1990–1997 and 2001–2005. + indicates captured in a given year.

Snake	1990	1991	1992	1993	1994	1995	1996	1997	2001	2002	2003	2004	2005
1	+	+	+										
2	+												
3	+	+											
4	+	+	+										
5	+	+											
6		+		+		+							
7		+											
8			+		+								
9			+										
10			+	+									
11			+			+							
12				+									
13				+									
14				+		+		+					
15				+									
16				+									
17					+								
18					+		+	+					
19					+		+						
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23						+		+					
24						+							
25							+	+					
26							+						
27								+					
28									+	+		+	
29									+		+		+
30									+	+			
31									+				
32										+			+
33										+	+		+
34										+			
35										+			
36										+	+		+
37											+	+	
38											+		
39												+	
40												+	
41													+
Total	5 (5 new)	6 (2 new)	6 (4 new)	7 (5 new)	5 (4 new)	7 (4 new)	5 (1 new)	5 (1 new)	4 (4 new)	7 (5 new)	5 (2 new)	4 (2 new)	5 (1 new)

(n=9), 22.2% did so in consecutive years, 33.3% in alternate years, and 44.4% in two consecutive years plus an additional year (Table 1).

Overall and yearly clutch size and female body size

There was no significant difference (Student *t*-test, df=130, P=0.096) in the mean total length of females at the communal oviposition site (mean=114.4±4.7 cm, range 104–127 cm) and those captured in the surrounding areas (i.e. at least 2 km from the study site but under the same climatic and habitat conditions; mean=113±5.2 cm, range 102–128 cm, n=59).

Fecundity was significantly correlated with female body size when the various years of study were pooled (r=0.697, n=41, ANOVA $F_{1,38}$=36.904, $P < 0.0001$) (Fig. 1).

There was no effect of the year of study on mean female size (one-way ANOVA: $F_{12,58}$=1.438, P=0.175; Fig. 2A), whereas there was a significant effect of the year of study on female fecundity ($F_{12,58}$=2.118, P=0.029; Fig. 2B). The year effect was increased (one-way ANOVA, with year as the factor and residuals as the dependent vari

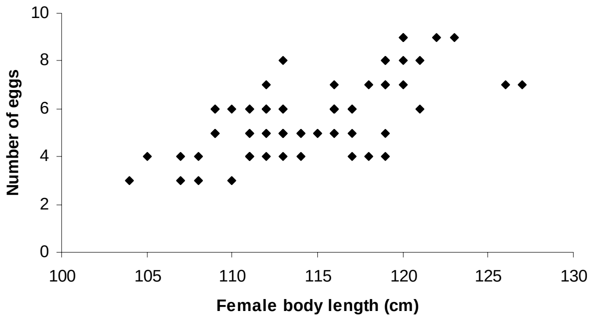

Fig. 1. Relationships between female size and fecundity (number of eggs) in *Hierophis viridiflavus* from the study area (data from all years pooled). Note that, although the total sample size is 41, the figure shows only 33 points as some include two or more specimens with exactly the same size and fecundity. For statistical details, see text.

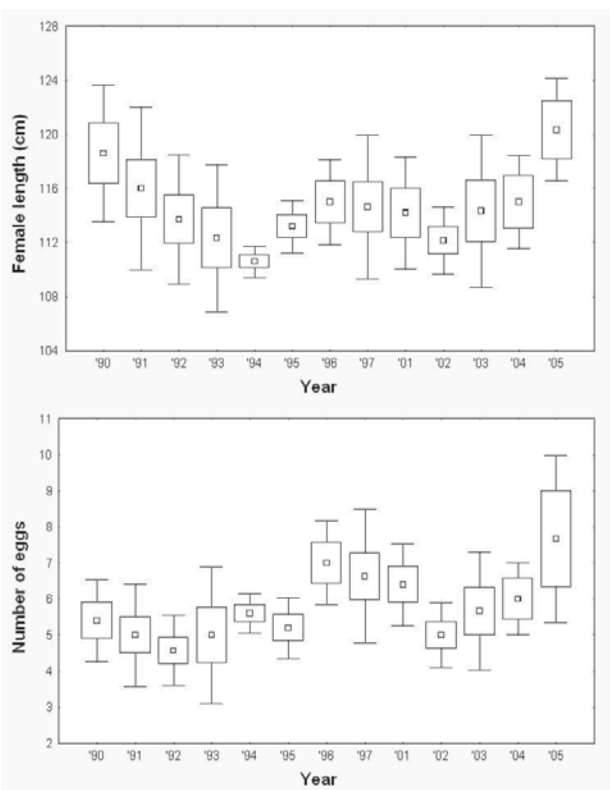

Fig. 2. Effect of year of study on female length (above) and female fecundity (below) in *Hierophis viridiflavus* from the study area. For statistical details, see text.

able; $F_{12,58}$=4.215, P<0.0001) when fecundity was corrected for female body size using the residuals of the general regression between maternal size and clutch size (Fig. 3). According to this analysis, the years 1996, 1997, 2001 and 2005 were particularly positive to produce a larger clutch, and 1990, 1991 and 1992 were particularly negative.

DISCUSSION

The overall relevance of this study is partially affected by 1) the fact that a single study area was used (i.e. lack of replicates) and 2) the sample size was not very big. These shortcomings are not uncommon in field studies of secretive animals, including snakes (Greene, 2001), and thus this study is not exceptional. Nonetheless, this is the first detailed long-term study (13 different years) on the ecology of communal oviposition in a species of European snake, and it has allowed us to respond quite reliably to the key questions posed in the introduction (see below). It is now evident that long-term studies may reveal important patterns in snake ecology that can remain masked during short-term studies (e.g. Madsen & Shine, 1992, 1993, 2001; Reading, 2004a).

Are communal oviposition sites used for prolonged periods by a given snake population?

At no time during our 13-year study did snakes fail to lay eggs in the study area, and in no year were there fewer than four females ovipositing at this site. In addition, during the interval between study periods, newborn snakes were observed in August, indicating that oviposition had occurred in the intervening years. Hence, there is no doubt that this communal oviposition site was regularly used by the snake population under study.

Is individual site fidelity or turnover rate high through the years?

Individual fidelity to the communal oviposition site was high, with more than 50% of the gravid females that were captured in the study area being recaptured in subsequent years (1–5 years), and always during the pre-oviposition phase. We also documented a constant turnover, with some females not captured in consecutive years and some new females being found during the pre-oviposition period. Although we know very little about the individual histories of females outside the oviposition period, we suggest that the non-capture of some females in some years was not the result of them selecting alternative oviposition sites but of them failing to reproduce. This is supported by the evidence that some females were captured regularly once every two years whilst others were captured in both alternate years and consecutive years (Table 1). It is known that the majority of females reproduce every year in the territories surrounding the study area (Capula et al., 1995, 1997).

The arrival of new females included cases of small (i.e. presumably young) individuals (<110 cm in length) who were probably breeding for the first time (i.e. individuals 6, 8, 12, 14, 16, 17, 19, 22, 27, 30, 39 and 40 in Table 1) as well as large, presumably older individuals (>120 cm; i.e. females 9, 26 and 32). These large individuals may have been present but missed by us, or they may have arrived at the oviposition site for the first time at a relatively old age. If this latter possibility is correct, further research is required to clarify when and why a given female decides to change its oviposition site at a later age whereas others start using the same oviposition site when they are

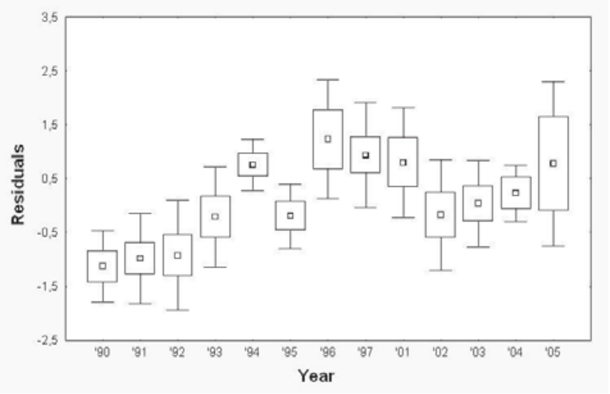

Fig. 3. Effect of year of study on the residual scores of the regression between maternal size and clutch size in *Hierophis viridiflavus* from the study area. For statistical details, see text.

young and then continue using it for years. In this latter case, it is also possible that these females simply do not show oviposition site fidelity.

On average, how many females used the communal oviposition site?

Although our study documented a yearly turnover of a portion of the female "population", the number of gravid females visiting the study site was remarkably constant across the years (usually 4–5, with a maximum of 7). The relatively low number of breeding females may be due to the occurrence of other oviposition sites around the study area (two found within 2.3 km of study site; see Capula & Luiselli, 1995).

Are communal oviposition sites used by a particular size category of females or more generally by all females?

It is evident from the body size comparisons between the gravid females visiting the study site and those randomly captured at other sites close to it that the communal oviposition site is not used preferentially by any specific size category of snakes. Overall, it seems that all females in the population (110–120 cm long) may regularly use the communal oviposition site.

Are there yearly differences in the body size and clutch size of females using the communal oviposition site?

Our study revealed that year had no effect on the mean body size of the females visiting the study site, but did on their fecundity, particularly after allowing for the relative body size of females. We consider that these results were influenced by more general conditions rather than by yearly differences at the study site per se. For example, we think that the higher fecundity recorded in some years compared to others depended on differences in the conditions experienced by females in those years (e.g. in the relative availability of prey), allowing them to store more energy reserves to invest in reproduction. Indeed, *H. viridiflavus* can be considered basically a "capital" breeder that needs to rebuild energy reserves for future reproduction because of the "costs"of reproduction (e.g. Madsen, 1983, 1987; Naulleau & Bonnet, 1996; Madsen & Shine, 1992, 1998, 2000; Bonnet et al., 1998; Lourdais et al., 2002; Shine, 2003), and in fact not all the females are able to reproduce every year (Capula et al., 1995). Also the longitudinal data collected in this study confirm that only some *H. viridiflavus* individuals are able to reproduce annually, while others reproduce in alternate years or even less frequently (Table 1), thus confirming the pattern of "irregular" reproductive frequency already highlighted in other species of snakes (e.g. *Vipera berus*, see Capula & Luiselli, 1994; *Coronella austriaca*, see Luiselli et al., 1996; Reading, 2004b).

More generally the positive relationship between female size and clutch size is consistent with those found for other European oviparous colubrids of comparable size (e.g. Naulleau, 1992; Naulleau & Bonnet, 1995).

What criteria are used by gravid female snakes in their selection of communal oviposition sites?

Three (not mutually exclusive) hypotheses can be offered to explain what may make a gravid *H. viridiflavus* select the study site as communal oviposition site. The study site provides 1) a good food source, 2) safe conditions due to a scarcity of natural predators and 3) conditions suitable for egg development (hence enhancing egg survival), being one of the few suitable nesting sites in a suboptimal area for the embryonic development of these snakes.

Although it is possible that all these reasons have some relevance for our study, it is convenient to examine each hypothesis in turn, in order to highlight which provides the best explanation for how snakes select communal oviposition sites.

Limited resource availability (i.e. scarcity of sites with conditions adequate for egg development). We suggest that the scarcity of suitable oviposition sites in the study area is certainly an important reason why many females selected the study site as communal oviposition site. There is some evidence supporting this hypothesis. Firstly, the study area is surrounded by closed-canopy forests (*Fagus sylvatica*) which are thought to be relatively unsuitable for these thermo-Mediterranean snakes; indeed these snakes tend to inhabit the less wooded open and drier sectors of the study area where the wooded cover is less, or the unwooded cultivated areas (Filippi, 1995). Secondly, inside the cultivated areas, where these snakes tend to be concentrated, the availability of burrows, stony walls or other sites suitable for egg-laying is low and hence many snakes are forced to use the few suitable sites.

Food. In theory, for the gravid snakes to select an oviposition place where prey are abundant may be important because food eaten during pregnancy, although not influencing the current reproductive effort, may contribute to post-oviposition female body condition and thus to her survival prospects (as in many species of snakes there is strong mortality associated with pregnancy costs, see Capula et al., 1992; Luiselli, 1992, 1995; Madsen & Shine, 1993, 2000; Luiselli et al., 1996) or even to her subsequent reproductive effort in the next year ("capital" breeding, see Shine, 2003). However, it is likely that most *H. viridiflavus* females stop feeding when heavily gravid (as in *Natrix natrix*, see Reading & Davies, 1996). If we take into account the dietary spectrum of *H. viridiflavus* in central Italy (see Capizzi & Luiselli, 1996), there are only two potential prey species at the study site, i.e. the wall lizards (*Podarcis muralis*) and the rats (*Rattus rattus*). The lizards are certainly less common than in many surrounding areas (Luiselli et al., unpublished data), whereas the rats are common but, apart from the newborn snakes, are too big to be eaten by most of the snakes (especially by the gravid females because of their pregnant condition). Therefore, we consider this hypothesis as extremely unlikely.

Safety. Compared to natural wooded areas, the oviposition site used by the snakes certainly has fewer natural predators, the only source of potential mortality for snakes being humans (who very rarely visit the dilapidated building and its immediate surroundings) and a few cats. We believe that this hypothesis may be valid for the study case.

In conclusion, therefore, we suggest that a combination of 1) limited availability of suitable oviposition sites and 2) safety factors may explain why female *H. viridiflavus* use the communal oviposition site at the study area. In addition, a recent experimental study (Brown & Shine, 2005) on the Australian egg-laying snake *Tropidonophis mairii* (Colubridae) has revealed that females selectively oviposited in sites containing empty eggshells rather than in control sites but did not avoid the scent of a sympatric egg predator (the slatey-grey snake, *Stegonotus cucullatus*); indeed, eggshells of this taxon were as effective as keelback eggs in attracting oviposition. This latter study adds to growing evidence that nesting females assess and respond to a diverse array of biotic as well as abiotic cues that predict the probability of successful incubation for their eggs, and it is possible that similar site assessment responses may also occur in the case of *H. viridiflavus* in our study area.

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