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Interpreting dispersal patterns of reproductive female *Hierophis viridiflavus* (LACÉPÈDE, 1789), around a communal nesting site
(Squamata: Serpentes: Colubridae)

Zur Verteilung weiblicher *Hierophis viridiflavus* (LACÉPÈDE, 1789) um einen gemeinschaftlichen Eiablageplatz in Abhängigkeit von ihrem Trächtigkeitsstatus
(Squamata: Serpentes: Colubridae)

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KURZFASSUNG

Die räumliche Verteilung adulter weiblicher Gelbgrüner Zornnattern, *Hierophis viridiflavus* (LACÉPÈDE, 1789) um einen gemeinschaftlichen Eiablageplatz wurde anhand von Informationen aus 17 Studienjahren untersucht. Dazu werteten die Autoren Fang-Wiederfang-Daten hinsichtlich der Entfernung aus, in der adulte Weibchen von einem gemeinschaftlichen Eiablageplatz gefunden wurden. Dabei ergab sich folgendes:

(1) Einige der reproduktiven Weibchen scheinen zwischen den Möglichkeiten einer Eiablage am gemeinschaftlichen Ablageplatz und einer Ablage an anderer Stelle wechseln zu können.

(2) Weibchen, die in einem gegebenen Jahr am gemeinschaftlichen Ablageplatz Eier legten, hatten sich im Jahr davor tendenziell in geringer Entfernung vom Eiablageplatz aufgehalten.

(3) Weibchen, die nach erfolgter Eiablage in schlechter körperlicher Verfassung.waren, wurden in größerer Entfernung vom gemeinschaftlichen Eiablageplatz wiedergefunden. Möglicherweise dient weiteres Umherstreifen zur Steigerung der Jagdeffizienz, sodaß Energiereserven vor der Überwinterung besser ergänzt werden können.

ABSTRACT

Using data acquired over 17 years, dispersal patterns around a communal nesting site (CNS) of adult females of the oviparous colubrid snake *Hierophis viridiflavus* (LACÉPÈDE, 1789), were investigated. The authors analyzed capture-mark-recapture data in terms of the distances at which adult females were found from their CNS i.e., oviposition place. The data revealed the following:

(1) Some reproductive females seem to be able to switch between the options of ovipositing at the CNS or elsewhere.

(2) Females who oviposited at the CNS in a given year were by trend observed at short distances from this oviposition site in the year before the effective nesting.

(3) Females of poor body condition after oviposition engaged in longer displacements from the communal nesting site, possibly to increase foraging efficiency and rebuild lost body reserves prior to entering brumation.

KEY WORDS

Reptilia: Squamata: Serpentes: Colubridae, *Hierophis viridiflavus*; communal nesting, movement behavior, Central Italy

INTRODUCTION

Recent studies of spatial ecology in free-ranging snakes revealed intriguing biological phenomena (e.g., see SHINE et al. 2001; CARFAGNO & WEATHERHEAD 2006) including the experimental demonstration of patterns previously supposed e.g., that snake dispersal is male-biased (KEOGH et al. 2007). Adult female snakes may exhibit unusual movement patterns because of their high ‘costs’ of reproduction (e.g., SHINE 1980; MADSEN 1987; BONNET et al. 2001). For example, gravid females may engage in long distance displacements to find suitable oviposition sites, which are scarce in cold climate regions (e.g., MADSEN 1983, 1987). Females of several species may oviposit in communal nesting sites (e.g., GORDON & COOK 1980; GOMILLE 2002) where they may return to lay eggs several times during their life (FILIPPI et al. 2007; LUISELLI et al. 2011).

The same communal nesting site may be used jointly by various species (LAPINI 1983). However, no data from outside the oviposition period is available regarding the movement patterns of females that lay their eggs at communal nesting sites.

By analyzing data compiled from 17 years of research (CAPULA & LUISELLI 1995; CAPULA et al. 1997; FILIPPI et al. 2007; LUISELLI et al. 2011; RUGIERO et al. 2012), the authors present a study on the movement patterns of female Western Whip Snakes for years in which they were not present at the communal nesting site. In the study, about half of the females inhabiting the study area came back year by year, or at least in alternate years, to lay eggs at the communal oviposition site (CAPULA & LUISELLI 1995; FILIPPI et al. 2007), whereas the other half was observed only once ovipositing at the communal nesting site (see Appendix 1 in LUISELLI et al. 2011). A reasonable assumption explaining this latter pattern implies that some females are unable to breed annually due to high energy costs of reproduction, (e.g., BONNET et al. 2001) and hence would not return to the communal oviposition site in such years. An alternative hypothesis is that the 'missing' females laid their eggs in places different from the communal nesting site.

In the present paper the authors examined which of the two above-mentioned hypotheses applies, and in addition, tested whether a female snake remains close to, or at some distance from, the communal nesting site in the years in which she does not oviposit there.

MATERIALS AND METHODS

Study species.- The Western Whip Snake, *Hierophis viridiflavus* (LACÉPÈDE, 1789) is a medium-sized (up to 150 cm long), oviparous, colubrid snake that feeds mainly upon lizards and small rodents (RUGIERO & LUISELLI 1995; LELIÈVRE et al. 2012). At the study area, this snake is above-ground active from March to November, and most of the females breed every year (FILIPPI et al. 2007; LUISELLI et al. 2011).

Study population.- The communal nesting site was used every year by snakes at least since 1990-2012, with a mean number of 5.46 gravid females visiting the CNS each year for egg-laying (FILIPPI et al. 2007). The CNS was visited only by gravid females and by a small number of males (FILIPPI et al. 2007), whereas newborn snakes were observed frequently after hatching (RUGIERO et al. 2012). Each gravid female visited the CNS for a mean of 2.2 years (FILIPPI et al. 2007), although some females visited the site in six years (LUISELLI et al. 2011). The period of egg-laying was, with some yearly variations, at the end of June to mid July. In the last years, most egg-laying events occurred in late June (RUGIERO, CAPULA, VIGNOLI & LUISELLI, unpublished). Population size at CNS, using the Jolly-Seber model, fluctuated between less than 10 (2003) and about 40 (1994 and 2004) (LUISELLI et al. 2011). Hatchlings were usually born by mid-August. Those which were lighter in weight tended to disperse farther than heavier hatchlings, whereas, after one year, there was no difference in body mass between the individuals that dispersed farther and those that remained near the CNS (RUGIERO et al. 2012).

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 is characterized by a partially dilapidated building (a cuboid stone building, measuring 5.0 m x 3.5 m, height 5 m) bordered by rich thorny vegetation (mainly *Rubus* spp.) and surrounded by cultivated fields and small oak (*Quercus cerris*) woodland patches. The climate of the study area is Mediterranean (TOMASELLI et al. 1973).

Field protocol.- Data given here were collected during a long-term study on the reproductive ecology of the Western Whip Snake around a communal nesting site (CNS), in 1990-1997 and 2001-2009 (FILIPPI et al. 2007; LUISELLI et al. 2011).

The study area consisted of a core area and a peripheral area. The size of the core area used for the capture-mark-recapture study was 3.0 ha (that roughly can be visualized by a circular area of about 100 m radius), the CNS being situated in the center (LUISELLI et al. 2011). In the core area, field effort per year was at least 12 days (hrs 0800-1800) in 1990-1997 and in 2001, and at least 24-28 days (hrs 0800-1800) in 2002-2009, with three people independently searching for snakes each day. Thus, the overall field effort was approximately 360 person hours per year in 1990-1997 and in 2001, and 720-840 person hours per year in 2002-2009. Additional searches, more irregularly distributed across the year, were also performed in the peripheral area. The whole area surveyed, including both the core and the peripheral, was 9.3 ha (that roughly can be visualized by a circular area of about 172 m radius), with the CNS being situated approximately in the center. Several observations of marked snakes included in this study refer to individuals spotted considerably outside the core and peripheral areas, which are part of a region employed by the authors for more than 20 years of studying the ecology and demography of *Vipera aspis* (LINNAEUS, 1758) (e.g., see RUGIERO et al. 2012).

Snakes were captured by hand and individually marked by ventral scale clipping (BROWN & PARKER 1976) for future identification. Females were palpated in the abdomen to verify their pregnancy status and to count the number of eggs according to the method outlined in FILIPPI et al (2007). Date of capture and both weight and length (SVL, precision ± 0.5 cm) were recorded.

The precise site of capture of each female was entered on a digital map using GPD, and its linear distance from the CNS was calculated by DIVA-GIS free software available at http://www.diva-gis.org/ (precision ± 1 m). For homogeneity across individuals, only one (the first) capture per individual and year was considered.

Due to the small size of the stone building used as CNS by snakes and the high field effort concentrated at the oviposition period (mostly end of June to mid-July; in later years chiefly in late June), it is likely that in all study years we captured the great majority (if not all) of the females reproducing at the CNS (FILIPPI et al. 2007; RUGIERO, CAPULA, VIGNOLI & LUISELLI, unpublished).

Statistical analyses.- Only those females (n = 57) entered the analyses which (i) had oviposited at the CNS at least once within the study period (see LUISELLI et al. 2011) but (ii) were not observed to arrive at the CNS for oviposition in the year when they were captured (n = 28; this study). The records were divided in three categories:

(1) marked females captured outside CNS while gravid in a given year and did not oviposit (i. e., were not observed) at CNS in that same year, and thus, were likely to have laid eggs at unknown sites different from CNS (type 1 females, n = 8). Occurrence of type 1 females documents that these individuals did not oviposit obligatorily at the CNS, although many of these snakes regularly returned to the CNS for oviposition in the study years (FILIPPI et al. 2007; LUISELLI et al. 2011);

(2) marked females captured outside CNS while non-gravid in a given year, but laid eggs (i. e., were observed) at the CNS in the following year (type 2 females, n = 12)

(3) marked females recaptured outside CNS in non-gravid status in the year following the year of oviposition at CNS (type 3 females, n = 8). Females of the latter categories could indicate migratory tendencies of snakes that have just laid eggs at the CNS (type 3 females) or that are going to lay eggs at the CNS (type 2 females) in the year following/preceding egg-laying at the CNS.

The authors compared the linear distances from the CNS of the sites at which type 2 and 3 females were found, to test whether the movement patterns adopted by a female in a given year (i.e., staying closer to, or farther from, the CNS) could predict her nesting activity in the following year.

Nonparametric statistics were used when normality (tested by Kolmogorov-Smirnov test) was not achieved in the examined variables. The differences in the mean distances from the CNS between type 2 and type 3 individuals were tested by Mann-Whitney U-test, and those between the three categories of individuals by Kruskal-Wallis ANOVA.

Logistic regression analysis was applied to discern whether or not the linear distance of capture from the CNS, recorded in a given year, would predict the occurrence of oviposition at the CNS in the fol-

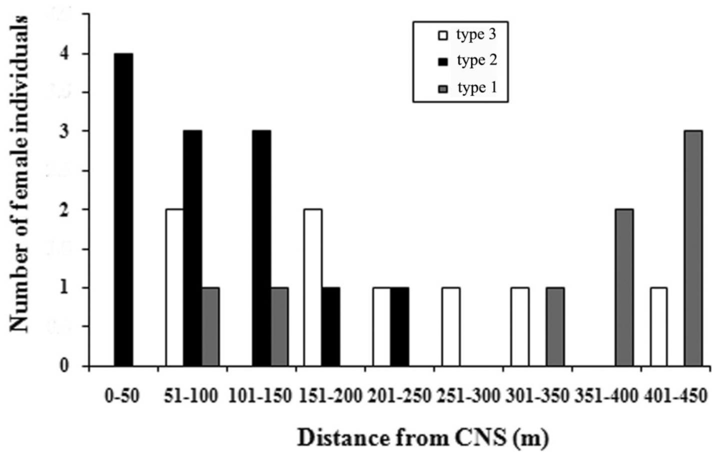

Fig. 1: Distribution of the distances (m) from the communal nesting site (CNS) at which female *Hierophis viridiflavus* (LACÉPÈDE, 1789) of types 1, 2 and 3, respectively, were found. Grey columns - type 1 females; black columns - type 2 females; white columns - type 3 females.

Abb. 1: Verteilung der Entfernungen (m) vom gemeinschaftlichen Eiablageplatz (CNS), in denen Typ 1, 2 und 3 Weibchen von *Hierophis viridiflavus* (LACÉPÈDE, 1789) gefunden wurden. Graue Säulen - Typ 1 Weibchen; schwarze Säulen - Typ 2 Weibchen; weiße Säulen - Typ 3 Weibchen.

lowing year. In this analysis, deposition/non-deposition of eggs at the CNS is the dependent variable, whereas the linear distance from the CNS at which each female was captured is the independent variable. For optimization, the simplex estimation method was used, with a maximum of 50 iterations and a 0.001 convergence criterion. A constant was included in the model (HOSMER & LEMESHOW 1989).

All analyses were performed with SPSS (version 8.0) statistical software package, with alpha assessed at 0.05 and all tests being two tailed. In the text, means are indicated ± 1 Standard Deviation.

RESULTS

Overall, eight type 1 females were captured, sighted at 319.1 ± 146.8 m from the CNS (median = 391; range: 73-445). The sample size is too small to reveal whether there was an effect of the year on the probability of recording individuals of this category at the study area.

The authors collected distance data for 12 type 2 and eight type 3 females. Distance ranges were 15-211 m in type 2 (median = 72.5), and 71-445 m in type 3 (median = 209.5) (Table 1). The ranges of type 1 and 3 females were almost identical, whereas their medians differed clearly. There was a clear trend for type 2 individuals to be captured closer to the CNS than individuals of types 3 and 1 (Fig. 1). Indeed, the average distances from CNS at capture of type 2 females (89.2 ± 65.7 m) were significantly lower than those of type 3 females (220.6 ± 123.5 m) (Mann-Whitney U-test: $Z = -2.733$, $U = 13$, $P < 0.005$). There were significant differences between females of types 1, 2 and 3 as for their distances of capture from the CNS (Kruskal-Wallis ANOVA: $H = 11.45$, $P = 0.00327$), with type 2 females being found at significantly lesser distances than both type 3 and 1 females, the latter being captured at similar distances from the CNS (Kruskal-Wallis ANOVA: $H = 2.01$, $P = 0.1559$).

Table 1: Information on 28 female *Hierophis viridiflavus* (LACÉPÈDE, 1789) captured and recaptured in the study area (Oriolo Romano, Viterbo, Italy). The snakes satisfy the selection criteria of (i) having oviposited in the communal nesting site (CNS) at least once within the study period and (ii) were not observed to arrive at the CNS for oviposition in the year when they were captured.

Tab. 1: Daten zu 28 im Untersuchungsgebiet (Oriolo Romano, Viterbo, Italien) gefangenen und wiedergefangenen Weibchen von *Hierophis viridiflavus* (LACÉPÈDE, 1789), die folgenden Auswahlkriterien genügten: (i) ihre Eiablage mußte innerhalb des Untersuchungszeitraumes zumindest einmal am gemeinschaftlichen Eiablageplatz (CNS) erfolgt sein und (ii) die Tiere durften im Jahr ihres Fanges nicht am gemeinschaftlichen Eiablageplatz angetroffen worden sein.

Snake ID Schlange Nr.	Category Kategorie	Capture date Fangdatum	Gravidity status yes/no = + / - Trächtigkeitsstatus ja/nein = +/-	Recapture date Wiederfangdatum	Gravidity status yes/no = + / - Trächtigkeitsstatus ja/nein = +/-	body length (cm) Körperlänge (cm)	linear distance from CNS (m) Entfernung vom CNS (m)
5	type 1	May 1993	+			107.0	73
5	type 1	May 1994	+			107.2	106
6	type 2	June 1992	-	May 1993	+	107.2	27
6	type 2	June 1994	-	June 1995	+	108.5	55
8	type 3	June 1994	+	June 1995	-	98.5	276
10	type 1	June 1995	+			93.8	316
11	type 3	June 1992	+	June 1993	-	115.7	194
11	type 2	June 1994	-	June 1995	+	118.0	110
14	type 2	June 1996	-	July 1997	+	106.0	150
18	type 2	June 1995	-	June 1996	+	115.2	15
18	type 1	June 2002	+			119.6	395
19	type 2	June 1995	-	June 1996	+	112.6	90
23	type 2	June 1996	-	July 1997	+	101.4	172
24	type 3	July 1995	+	June 1996	-	105.0	311
25	type 1	June 2002	+			120.5	420
26	type 3	May 1996	+	June 1997	-	106.3	225
29	type 2	June 2002	-	June 2003	+	98.5	51
30	type 2	June 2004	-	June 2005	+	102.0	34
31	type 1	July 2003	+			117.4	411
32	type 2	June 2004	-	June 2005	+	96.8	134
37	type 2	June 2004	-	June 2005	+	97.0	211
41	type 3	June 2003	+	June 2004	-	100.5	87
41	type 1	June 2006	+			102.2	387
43	type 1	June 2008	+			97.7	445
44	type 2	June 2004	-	May 2005	+	89.6	21
48	type 3	June 2006	+	May 2007	-	88.8	156
49	type 3	June 2006	+	June 2007	-	96.0	445
54	type 3	June 2008	+	June 2009	-	97.5	71

A logistic regression model (-2 log Likelihood = 17.992; Goodness-of-fit = 16.537; χ^2= 9.533, *df* = 1, *P* < 0.002) revealed that the distance from CNS at a given year was a good predictor of the occurrence of oviposition at the CNS in the following year (80 % of cases correctly classified; *Beta* = - 0.194, *r* = - 0.328, *P* = 0.026).

DISCUSSION

The capture-mark-recapture data showed that:

(i) some gravid female *Hierophis viridiflavus* that oviposited at least once at the CNS did not obligatorily do so over the years and must have oviposited also in places different from the CNS (type 1 females);

(ii) these type 1 females were usually found at considerable distances from the CNS;

(iii) females which oviposited at the CNS in a given year tended to be found at short distances from the CNS in the year before (type 2 females); and

(iv) females captured in non-reproductive state in the year after oviposition at the CNS (type 3 females) were more frequently observed comparatively far from the CNS.

Concerning item (i), it is unknown what makes a female snake select on whether to oviposit at the CNS or elsewhere. Results from items (iii) and (iv) indirectly suggest that many females ovipositing at the CNS do not engage in long displacements finding their nesting site, as observed in other oviparous snakes, including e.g., Grass Snakes *Natrix natrix* (LINNAEUS, 1758), from Sweden (MADSEN 1984, 1987). These patterns are also confirmed by the logistic regression analysis clearly showing that distance of capture from CNS of a given female in a given year predicts her oviposition at the CNS in the following year.

We have no direct evidence of the reasons behind the fact that type 3 females were found at distances from the CNS significantly greater than observed in type 2 females. We hypothesize that those females are in poor body condition after oviposition (type 3) because of the high costs of reproduction (SHINE 1980; MADSEN 1987; BONNET et al. 1999, 2002) and thus engage in longer displacements from the CNS in order to increase foraging efficiency, thereby rebuilding lost body reserves prior to brumation. The above-mentioned hypothesis is based on the finding, at the same *H. viridiflavus* population, that hatchlings in poor body condition were found at a longer distance from their birth place than heavier ones (RUGIERO et al. 2012). They probably moved away to increase their foraging efficiency, a strategy that paid off well for the one-year old hatchlings that were pretty light at birth (RUGIERO et al. 2012).

The hypothesis that the more emaciated post-oviposition females (i.e., those which were unlikely to reproduce again in the year following oviposition) moved farther away from the CNS than the less emaciated ones, is in agreement with the results of this study (type 3 females). Accordingly, these females would not reproduce every year, but only every second or third year, and, during the non-gravid period, accumulate energy to be invested in reproduction in the following years. This pattern is classic in temperate zone snakes, especially when trophic resources are not abundant (e.g., SHINE 1980; CAPULA & LUISELLI 1994; GREGORY et al. 1999; BONNET et al. 2002). Moreover, the Western Whip Snake has very high energy requirements (see LELIÈVRE et al. 2010b).

In the study area, 66.7 % of the female individuals were recaptured while laying at the CNS in consecutive years (FILIPPI et al. 2007) confirming an annual reproduction frequency, and only 33.3% of the females visiting the CNS did so in alternate years (FILIPPI et al. 2007), apparently being compatible with the hypothesis of a biannual reproductive frequency (note that however these estimates are partially biased by the type 1 females, which were gravid but did not reproduce at the CNS in all years).

Other studies conducted in the same region confirmed that most females of the

Western Whip Snake lay eggs annually (frequency of annual breeders estimated to be at about 75 % of the total number of adult females; CAPULA et al. 1995), with considerable within-population individual variation due to the different body condition of post-reproductive females (CAPULA & LUISELLI 1994). Concerning the dietary spectrum of *H. viridiflavus* in central Italy (see CAPIZZI & LUISELLI 1996), there are only two potential prey species at the CNS, wall lizards *Podarcis muralis* (LAURENTI, 1768), and rats (*Rattus rattus*) (see FILIPPI et al. 2007) and it is very likely that snakes remaining at the CNS after oviposition may have little opportunity to rebuild their depleted body fat reserves. *Hierophis viridiflavus* is an active hunter who can make important movements to feed (LELIÈVRE et al. 2010a), so it is very likely that distance traveled may be correlated to hunting success.

In conclusion, the analysis of long-term data revealed a scenario where the advantages provided by the stone building for communal reproduction of snakes (i.e., good incubation conditions and low predation risks; see FILIPPI et al. 2007) are partially counterbalanced by the costs of the relatively low prey availability. Depending on their own body condition, the female strategy shifts between repeated oviposition at the CNS (strategy used by females in good body condition) to occasional use of the CNS and reproduction in alternate years (used by females in suboptimal body condition). These latter females would be forced to search for food in sites where trophic resource availability is higher than at the CNS.

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