Life-history and diet of two populations of *Natrix maura* (Reptilia, Colubridae) from contrasted habitats in Sardinia

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Life-history and diet of two populations of Natrix maura *(Reptilia, Colubridae) from contrasted habitats in Sardinia.*– Aspects of general ecology and population biology of two populations of free-living viperine snakes (*Natrix maura*) were studied in Mediterranean localities of the island of Sardinia (Thyrrenian Sea, Italy). The apparent adult sex-ratio was not significantly different from equality, but males were slightly more numerous than females. The diet consisted mainly of amphibians, both adults and tadpoles (area A) or fish (area B). Females were significantly longer than males. Reproduction was yearly, and clutch size and female total length were positively correlated. A hundred and seven live offsprings were obtained from 135 eggs (79.2% of successful incubation rates). The proportion of unsuccessful incubation was not significantly correlated with either female total length or clutch size. There was no evidence of a trade-off between clutch size and offspring size, as hatchlings were no smaller in clutches that were unusually large in relation to maternal body size. Oviposition date was correlated with neither maternal length nor clutch size. Incubation period was significantly correlated with mean hatchling size, but not with either clutch size or maternal length. No female died after oviposition, thus suggesting a very low incidence of mortality rates due to starvation and reproductive costs. A case of long-term sperm storage deriving from autumnal mating is described. Population size estimates are provided for both study areas.

Key words: *Natrix maura*, Ecology, Mediterranean region, Sardinia.

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Introduction

Field studies on the ecology of European Natricinae (Serpentes, Colubridae) have received considerable attention during recent years either because of their remarkable phenotypic plasticity in life-history traits or due to their abundance in the field which enables testing of relevant hypotheses and highlighting of general ecological patterns (MADSEN, 1983, 1987; MADSEN & SHINE, 1993a, 1993b). Most of these studies dealt with the grass snake *Natrix natrix*, which has been extensively studied particularly in Sweden and in Italy (MADSEN, 1983, 1987; MADSEN & SHINE, 1993a, 1993b; LUISELLI & RUGIERO, 1991; LUISELLI, 1996; LUISELLI et al., 1997). The viperine snake *Natrix maura*, an oviparous species with a wide distribution across western Europe, has also received much attention from scientists, and highly detailed ecological data are available for one Spanish population (HAILEY & DAVIES, 1986a, 1986b, 1986c, 1986d, 1987a, 1987b, 1987c, 1987d). However, nothing is known on the *N. maura* population inhabiting the island of Sardinia in the Thyrrenian Sea, despite the fact that these island populations could differ genetically from mainland populations, and their origin is unknown. In this paper, data on various aspects of the ecology of two viperine snake populations from contrasted habitats in Sardinia are presented and compared with information of populations of the genus *Natrix* from elsewhere.

Materials and methods

Study areas

This study was carried out at two localities in Sardinia (fig. 1).

Locality A
"Giara di Gesturi", about 270 km south-west of Nuoro, 550 m a.s.l. Is characterized by large freshwater ponds within grassy pastures interspersed with dense bushes (*Pistacia lentiscus, Myrthus communis, Phillyrea angustifolia*, etc.). This area is typically Mediterranean, with rainfall concentrated in early spring and late autumn, and hot dry summers. The total study area

was 11.2 ha, including both ponds and surrounding land. In this study area, *N. maura* is extremely common within and around the ponds. The only other snake species of the area, *Coluber viridiflavus*, is widespread, but in terrestrial habitats only. Two anuran species have been found in the ponds: *Hyla sarda* and *Discoglossus sardus*.

Locality B
"Santa Margherita di Pula", about 35 km south-west of Cagliari, 0 m a.s.l. Is a tourist centre on the Thyrrenian coast. The study area was characterized by small artificial ponds interspersed among private gardens. These garden ponds were generally less than 20 m². Five of these ponds were surveyed for snakes. The total surveyed area, including both the ponds and the surrounding land, was 37 ha. Small numbers of snakes were found in some of these artificial ponds. *H. sarda* was common and *D. sardus* was extremely rare. Introduced ornamental fish species (*Carassius auratus* var. *domestica* and *Gambusia affinis*) were found in all ponds. In one pond, introduced red-eared terrapins (*Trachemys scripta elegans*) were observed. These turtles could not be considered as potential predators of the snakes because of their diet.

Methods

Surveys for snakes were carried out, at irregular intervals of time between June 1993 and October 1996 in area (A), and in March 1999 in area (B). Additional incidental observations of the snakes in this latter area were sparsely made during the years 1981-1985. The snakes were captured by hand, individually marked by ventral scale-clipping, measured for total length (TL, to the nearest ±0.1 cm), weighed by electronic scales (precision ±0.1g), sexed by analysing the external tail morphology (FERICHE et al., 1993), and palpated in the abdomen to determine whether they had prey in the stomach as well as to determine their reproductive status in the case of females. Since length and mass were highly correlated in both males and females (in both sexes and in both areas, total length versus cubic root of body mass, $r > 0.8$, $P < 0.00001$), here we limit our analyses to lengths only. When presence of
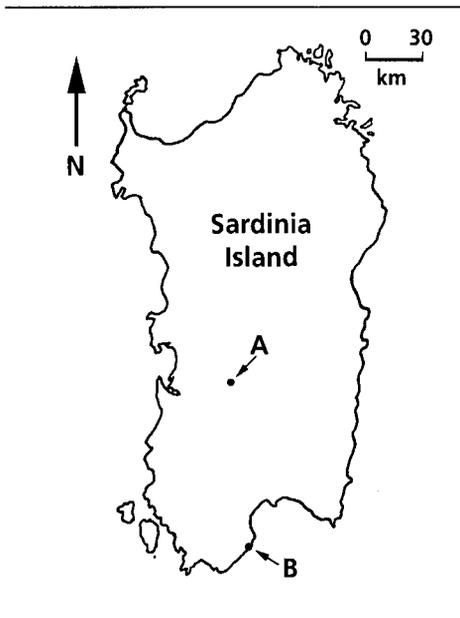
Fig. 1. Map of Sardinia showing the two study areas: A. Giara di Gesturi, province of Nuoro; B. Santa Margherita di Pula, province of Cagliari.

Mapa de Cerdeña mostrando las dos áreas de estudio: A. Giara di Gestrui, provincia de Nuoro; B. Santa Margherita di Pula, provincia de Cagliari.

any food item in the stomach was detected, the snake was squeezed in order to constrain him to regurgitate the ingested bolus. This procedure is easily performed and is totally harmless for the handled individuals. Gravid females were removed from the natural environment and housed in indoor terraria (100x40x40 cm) for studying clutch parameters. These indoor enclosures were lighted by "Gro-lux" fluorescent lamps (40 W); humidity was maintained at 80%. Food (tadpoles and green froglets) was provided. Eggs were incubated in vermiculite as reported by Townson (1990). All individuals, both mothers and their litters, were released at the spot of capture at the end of our study. "Post-oviposition" mortality rates of reproductive females were estimated by using the procedure in Luiselli (1992) and in

Luiselli et al. (1997), i.e. by maintaining the post-partum females in captivity for thirty days after oviposition.

Five adult females were collected during October 1992 (i.e. shortly before the beginning of hibernation) and maintained one year in captivity without males in order to assess the eventual occurrence of long-term sperm storage (LTSS, see also Capula & Luiselli, 1997). The occurrence of LTSS could be important in a species as *N. maura* which (i) is also known to mate during autumn (Naulleau, 1984), and (ii) some cases of exceptional survival of spermatozoa have been reported within the genital tracts of its females (Quillon & Lamouille, 1978).

Statistical analyses

In the text the means are followed by ± one Standard Deviation. Analyses were done by using SPSS/PC for Windows statistical software. All tests used were two-tailed, with alpha set at 5%. Population size was calculated by applying the formula:

$$N = A (n + 1) / (a + 1)$$

where N is the population size, A is the number of marked individuals in the first sample, n is the total number of individuals in the second sample, and a is the number of recaptured individuals in the second sample (Seber, 1982).

Pond size was measured in order to estimate the density of snakes, as this species is aquatic and rarely abandons water bodies and streams. Therefore, to calculate the population density, the total pond surface was considered, including a boundary strip of 10 m width right around the perimeter of each pond.

Results

Adult sex-ratio

Area A
During 1993, 44 adult specimens, 23 males and 21 females, were captured. During 1996, 24 adults, 14 males and 10 females, were captured. Juveniles smaller than 32 cm were not considered in these counts. The adult sex-ratio was not significantly different from equality in

either study year (1993: $\xi^2 = 0.09$, $d.f. = 1$, $P > 0.75$; 1996: $\chi^2 = 0.67$, $d.f. = 1$, $P > 0.4$).

Area B
In total, 15 adult males and 14 adult females were captured, with a secondary adult sex-ratio close to 1:1.

Food habits

Area A
Forty-five dietary records from 110 handled specimens (including both single captures and recaptures) were obtained. Considering that some snake specimens contained more than one prey item in the stomach, the proportion of snakes with recently ingested food was 28%. Table 1 summarizes the data collected: amphibians (both tadpoles and metamorphs) constituted the main proportion of the diet (86.6%); reptiles were very rarely preyed upon, whereas the main diet of juvenile snakes consisted of earthworms (60%). Contingency table analysis revealed no statistically significant differences between sexes in taxonomical composition ($P = 0.357$), but the examined sample was too small to confirm it.

Area B
Twenty (38%) of 53 handled specimens had food in the stomachs and a total of 34 prey items were collected (see table 1). The proportion of fed animals was statistically higher in area B than in area A ($\chi^2 = 28.61$, $d.f. = 1$, $P < 0.0001$). Fish represented the main prey source (82%), whereas *H. sarda* were rarely preyed upon (table 1). The two populations differed significantly in terms of taxonomical dietary composition ($\chi^2 = 42.96$, $d.f. = 7$, $P < 0.0001$).

Body sizes of males and females

Area A
Two-way ANOVA of TL by sex and year produced a significant model (F = 56.77, $d.f. = 2,71$, $P < 0.01$). Females were longer than males (males: $\bar{x} = 46.7 \pm 8.5$ cm; females: $\bar{x} = 54.9 \pm 10.9$ cm, Tukey test $P < 0.0005$), and TLs of both males and females were significantly longer in 1993 than in 1996 (Tukey test $P < 0.01$ in both sexes) despite the fact that in both years, only specimens longer than 32 cm TL were used in the analysis (1993: males $\bar{x} = 49.5 \pm 4.8$ cm, females $\bar{x} = 58.8 \pm 1$ cm; 1996: males $\bar{x} = 43.2 \pm 10.5$ cm, females $\bar{x} = 48.2 \pm 12.2$ cm).

Immature animals in the population accounted in total for 21.6% ($n = 74$) of the total number of marked specimens, and for 17.1% ($n = 41$) of the males and for 27.3% ($n = 33$) of the females. The intersexual difference was marginally significant ($\chi^2 = 3.57$, $d.f. = 1$, $P = 0.057$).

Area B
Two-way ANOVA by sex and population produced a significant model (F = 38.87, $d.f. = 2,111$, $P < 0.05$). However, significance was only due to intersexual size differences (Tukey test $P < 0.001$; females in area B, $\bar{x} = 63.2 \pm 9.2$ cm, males in area B, $\bar{x} = 47.7 \pm 11.6$ cm), and no difference in body length appeared between the two localities either in females nor in males (Tukey test n. s .).

Immatures accounted for 17.1% ($n = 35$) of the total number of marked specimens.

Density and population size

Although our trapping schedule was opportunistic and does not completely fulfill Lincoln-Petersen requirements, it provides a rough estimate of population size which is sufficiently adequate for the purpose of the paper.

Area A
During 1993, a total of 68 specimens (including both adult and immature animals) was marked, 26 specimens (for a total of 42 recaptures) were recaptured, and 18 additional specimens were observed. Thus, the population was estimated to consist of approximately 97 individuals, for an average density of 8.7 specimens ha^{-1}. Based on our 1996 data (30 marked specimens, 10 recaptured specimens, and 42 observed specimens), the population was estimated to include 117 individuals, for an average density of 10.5 specimens ha^{-1}, including both adult and immature specimens in this count.

Area B
During 1999, 35 specimens were marked,

16 specimens were recaptured, and 11 additional specimens were observed. The total population size was estimated to be 49.6 specimens, and the density was approximately 1.3 specimens ha^{-1}.

Density estimations herein should be considered an initial approach only, as more detailed research is essential before definitive conclusions can be reached.

Reproductive biology of females

Area A

Fifteen of 21 adult females (TL > 50 cm) collected during June 1993 were gravid. Thus, the proportion of breeding (71.4%) was significantly higher ($\chi^2 = 3.857$, $d.f. = 1$, $P < 0.049$) than the theoretical proportion expected for a biennial breeder (50%), which suggests an average annual frequency of female reproduction in the study area.

Mean clutch size was 8.8±2.7 eggs ($n = 15$); mean incubation period was 44.6±4.9 days ($n = 15$); mean oviposition date, counted after 20 June, was 10.7±2.1 ($n = 15$).

Clutch size and total female length were positively correlated ($r^2 = 53.36\%$, ANOVA $F_{1,13} = 14.87$, $P = 0.002$; see figure 2). One hundred and seven live offspring were obtained from 135 laid eggs (79.2% of successful incubation rates). The proportion of successfully incubated litters ranged from 100% to 37.5%. Proportion of unsuccessful incubation was not significantly correlated either with female total length (adjusted $r^2 = 11.8\%$, ANOVA $F_{1,13} = 2.881$, $P = 0.113$) or with clutch size (adjusted $r^2 = 16.9\%$, ANOVA $F_{1,13} = 3.848$, $P = 0.072$).

Mean size of the eggs at oviposition was 29.6 x 19.5 cm. Mean offspring TL per litter ranged from 15.2 to 18.3 cm. Mean offspring TL was not related to female TL ($r = 0.34$, $r^2 = 11.51\%$, ANOVA $F_{1,13} = 1.69$, $P = 0.216$; fig. 3). There was no significant relation between mean offspring TL per litter and clutch size ($r = 0.094$, $r^2 = 16.46\%$, ANOVA $F_{1,13} = 0.118$, $P = 0.736$). There was no evidence of a trade-off between clutch size and offspring size, as hatchlings were no smaller in clutches that were unusually large relative to maternal body size (testing

Table 1. Summary of the dietary data collected from *Natrix maura* individuals of the studied localities in Sardinia: L. Lumbricidae; Ga. *Gambusia affinis*; Ca. *Carassius auratus*; Ds-t. *Discoglossus sardus* tadpoles; Ds-m. *Discoglossus sardus* metamorp.; Hs-t. *Hyla sarda* tadpoles; Hs-m. *Hyla sarda* adults; Pt-a. *Podarcis tiliguerta* adult.

Datos dietéticos de individuos de Natrix maura *de las localidades de estudio en Cerdeña. (Para las abreviaturas ver arriba.)*

Prey	Area A N	Area B N
Oligochaeta		
L	5	1
Pisces		
Ga	-	21
Ca	-	8
Amphibia		
Ds-t	11	-
Ds-m	2	-
Hs-t	11	-
Hs-a	15	4
Reptilia		
Pt-a	1	-
Total	45	34

hatchling mass against residual scores from the regression of clutch size on maternal body length: $n = 15$, $r = 0.17$, $P = 0.62$).

Area B

No reproductive data were collected from area B.

Occurrence of long-term sperm storage (LTSS)

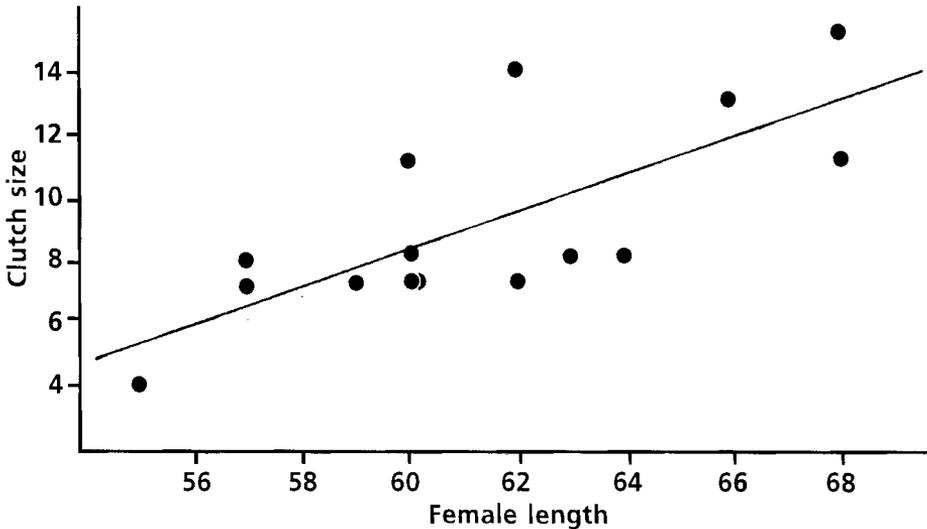### Area A

LTSS occurred in one out of five females

Fig. 2. Relationships between clutch size and female total length in *Natrix maura* from the study area A. For statistical details, see the text.
Relación entre el tamaño de la puesta y la longitud total de la hembra en Natrix maura *del área de estudio A. Para los detalles estadísticos, ver el texto.*

used in the experiment. This female was 58.3 cm TL, and deposited seven eggs on 3 July 1993. Mean egg size at the time of oviposition was 27.8 x 15.9 mm, a measure which was significantly smaller than that of the eggs obtained from other *N. maura* litters, which probably derived from spring matings ($P < 0.05$, two-tailed Student t-test). However, one offspring hatched from these eggs (7 August 1993); it was 17.2 cm long and appeared to be in good conditions.

Area B
No data on the occurrence of LTSS were collected from area B.

Discussion

This study revealed several life-history traits of these Sardinian *N. maura* populations that could be usefully compared with the same traits recorded from other Palearctic snake populations. To begin with, the adult sex-ratio was not significantly different from equality. This finding is in agreement with most studies on snakes published to date (e.g. see LUISELLI & ANGELICI, 2000). With regard to other *N. maura* populations, the adult sex ratio was not statistically skewed either in southeastern Iberian peninsula (PLEGUEZUELOS & MORENO, 1989), or in France (DUGUY & SAINT GIRONS, 1966). With regard to Natricinae species, highly skewed sex-ratios (with males more numerous than females) are known to occur during the spring mating season, immediately after the end of the hibernation, when virtually all the males emerge before the females, whereas the females emerge over a comparatively longer period (JOY & CREWS, 1988; MASON et al., 1989; MADSEN & SHINE, 1993a; FILIPPI et al.,1996; LUISELLI, 1996; LUISELLI et al., 1997). This pattern does not appear to be typical in Sardinian *N. maura*. In fact, although our data in this issue are not exhaustive, one of the two areas was surveyed in early spring (March 1999), i.e. probably earlier
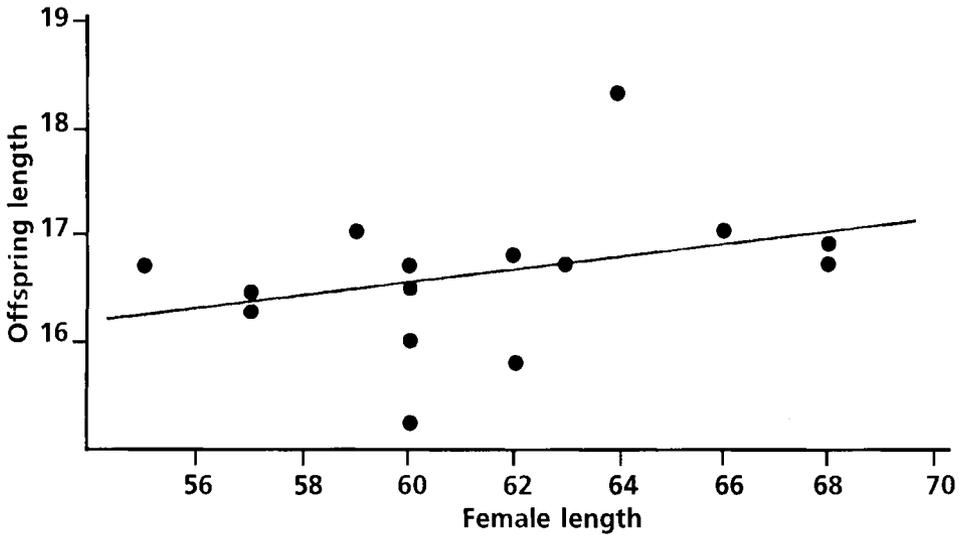
Fig. 3. Relationships between mean offspring length and female total length in *Natrix maura* from the study area A. For statistical details, see the text.

Relación entre la longitud media de los descendientes y la longitud total de las hembras en Natrix maura *del área de estudio A. Para los detalles estadísticos, ver el texto.*

than the onset of the mating season, but the adult sex-ratio was still very close to equality.

Data collected on food habits indicate that Sardinian *N. maura* are essentially opportunistic predators, but with a general preference for fish and amphibians. They were batracophagous in area A, but were piscivorous in the small artificial water bodies of area B where fish constituted an abundant food resource. Considering that ponds are common ornamental objects of gardens in Sardinian touristic villages, and that both *Carassius* and *Gambusia* are always introduced by landlords in these ponds (to beautify the pond and also to combat mosquitos), it is likely that many small populations of *N. maura* can establish viable metapopulations dispersing from main rivers and natural water bodies where these snakes are extremely abundant. These small populations could be ideal models to study the dynamics of colonization and dispersion of these pioneer snakes, which are extremely common and

widespread throughout the study regions (ENTOMOSARDA S.N.C., 1993). Batracophagy was previously observed in conspecifics from France (DUGUY & SAINT GIRONS, 1966; NAULLEAU, 1984), but Spanish *N. maura* proved to be mainly piscivorous (HAILEY & DAVIES, 1986a, 1986b). The potentially very eclectic diet of this species was well demonstrated in a large study conducted in the southeast Iberian peninsula, in which these snakes fed mainly upon earthworms, with fish and frogs taken as secondary prey items (PLEGUEZUELOS & MORENO, 1989). Thus, as a general rule, it could be hypothesized that diet eclectivity is a major component of the ecological success of *N. maura* in Mediterranean freshwater environments, as demonstrated by its extreme abundance all over of Sardinia (SCHATTI, 1982; PUDDU et al., 1988), and by its ability to adapt the diet even to drastic fluctuations in the water level in the ponds (SANTOS & LLORENTE, 1998).

The reversed sexual size dimorphism of Sardinian populations mirrors data available

on conspecifics from elsewhere (e.g. Duguy & Saint Girons, 1966; Schätti, 1982; Feriche & Pleguezuelos, in press) and on other *Natrix* populations from elsewhere, including e.g. *N. natrix* (Madsen, 1983; Gentilli & Zuffi, 1995; Luiselli, 1996; Luiselli et al., 1997) and *N. tessellata* (Filippi et al., 1996; Zimmermann & Fachbach, 1996). However, contrary to that which occurs in other snake species with significant sexual size dimorphism (cf. Shine, 1986; Luiselli & Angelici, 1998), Sardinian *N. maura* populations did not exhibit remarkable intersexual differences in taxonomic food composition (although the examined sample was too small to confirm this finding).

The fact that females in population A showed an annual frequency of reproduction is in clear agreement with data available for other populations of oviparous colubrids from Mediterranean Italy (e.g. *Elaphe longissima* and *E. quatuorlineata*, see Capizzi et al., 1996; *Coluber viridiflavus*, see Capula et al., 1997; *Coronella girondica*, see Agrimi & Luiselli, 1994; *N. tessellata*, see Luiselli & Zimmermann, 1997). In any case, European snakes of the genus *Natrix* usually produce one clutch per year even in cool and cold climates (Madsen, 1987; Luiselli et al., 1997), even though they may occasionally reproduce once every two years (e.g. *N. tessellata* in Austria, cf. Luiselli & Zimmermann, 1997). Annual frequency of reproduction was also obvious in *N. maura* females from southeastern Spain (Feriche & Pleguezuelos, in press). The positive relationship between clutch size and female length seen in Sardinian *N. maura* females is not surprising, this trend being rather universal in snakes in general, and in *N. maura* in particular (e.g. see Feriche & Pleguezuelos, in press). The number of eggs relative to female length was similar to that observed by Feriche & Pleguezuelos (in press) in Spanish *N. maura*, although the smallest Sardinian females carrying eggs (55 cm long) were bigger than the smallest reproductive Spanish females (about 30 cm, see Feriche & Pleguezuelos, in press). This difference could be merely an artifact of the different sample sizes, as Feriche & Pleguezuelos (in press) were able to examine a much larger sample of gravid females.

Correlates of the incubation period of Sardinian *N. maura* population strongly mirror data for some other populations of congenerics, i.e. *N. natrix* from the Italian Alps (cf. Luiselli et al., 1997). In fact, in neither population were the oviposition date and the incubation period correlated with either maternal size or clutch size. But the most interesting similarity between the two congeneric populations is that a more prolonged incubation produced longer hatchlings. In agreement with Olsson et al. (1996) and with Luiselli et al. (1997), we suggest that hatchlings emerging after longer incubation periods are longer than those emerging after shorter incubation periods because they have had more time in which to convert yolk reserves into body tissue. These two *Natrix* populations were also similar in that there was no correlation between (1) proportion of non-viable eggs and maternal length, (2) proportion of non-viable eggs and clutch size, and (3) maternal length and mean hatchling length (cf. also data in Luiselli et al., 1997).

The present study also shows that, contrary to other temperate zone species (e.g. *Vipera berus*, see Luiselli, 1993, 1995), *N. maura* can use long-term sperm storage as an alternative (to spring mating) mating strategy. However, the present data cannot determine whether or not such an alternative strategy is important for the free-ranging populations of this species. In any case, the fact that the climate in the study area (Mediterranean) is very mild even in October-November could easily permit an autumnal mating phase to *N. maura*, thus giving the basic conditions where long-term sperm storage can evolve (cf. Capula & Luiselli, 1997).

Several snake populations from temperate regions exhibit remarkable costs of reproduction in terms of both energy and survival (e.g. see Madsen, 1987; Luiselli, 1992; Madsen & Shine, 1993c; Capula & Luiselli, 1994; Luiselli et al., 1996, 1997). Did Sardinian *N. maura* populations show significant costs of reproduction? Since we have no measurements of RCM (Relative Clutch Mass), we cannot make firm conclusions on this issue. However, we have no direct indication of female mortality after egg-laying, which suggests moderate costs of reproduction in this population. In fact, female mortality after parturition (or egg-laying) is a common occurrence in snake populations (which are

usually live-bearing species) submitted to high costs of reproduction (e.g. *V. berus* and *C. austriaca*, cf. LUISELLI, 1992; MADSEN & SHINE, 1993c; LUISELLI et al., 1996).

Resumen

Life-history y dieta de dos poblaciones de Natrix maura *(Reptilia, Colubridae) de hábitats contrastados de Cerdeña.*

Se estudian aspectos de ecología general y de la biología de población de dos poblaciones de serpientes viperinas (*Natrix maura*) en estado libre en localidades mediterránea de la isla de Cerdeña (mar Tirreno, Italia) (fig. 1). El procentaje de sexos parece no ser significativamente diferente, pero los machos son ligeramente más numerosos que las hembras. La dieta consiste básicamente en anfibios, tanto adultos como renacuajos (área A) o peces (área B) (tabla 1). Las hembras son significativamente más largas que los machos. La reproducción es anual y el tamaño de la puesta y la longitud total de la hembra estan correlacionados positivamente (fig. 2). De 135 huevos se han obtenido 107 descendientes vivos (79,2% de porcentaje de incubación con éxito). La proporción de incubaciones no exitosas está correlacionada significativamente con la longitud total de la hembra o con el tamaño de la puesta. No hay evidencia de relación entre el tamaño de la puesta y el tamaño de los descendientes (fig. 3) ya que las eclosiones no han sido inferiores en puestas que eran inusualmente grandes en relación al tamaño corporal de la madre. La fecha de oviposición no está correlacionada ni con la longitud de la hembra reproductora ni con el tamaño de la puesta. El periodo de incubación está correlacionado significativamente con la media de las eclosiones pero no con el tamaño de la puesta ni la longitud de la madre. Ninguna hembra murió después de la oviposición, lo que sugiere valores muy bajos de mortalidad a causa de la inanición y los costes reproductivos. Se describe un caso de almacenamiento prolongado de esperma debido a un apareamiento otoñal. Se proporcionan los tamaños estimados de las poblaciones de las dos áreas de estudio.

Acknowledgements

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