

BREEDING FREQUENCY, CLUTCH SIZE, REPRODUCTIVE STATUS
AND CORRELATED BEHAVIOURS IN SYMPATRIC FEMALES
ELAPHE QUATUORLINEATA AND *ELAPHE LONGISSIMA*
(REPTILIA : COLUBRIDAE)

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INTRODUCTION

Field-studies on the reproductive biology of snakes have traditionally dealt with given reproductive parameters (e.g. clutch size, relative clutch mass, offspring size, etc.) recorded at a given point in time (« cross-sectional » studies) (Seigel & Ford, 1987), while scarce attention has been given to the variation in the same reproductive parameters of one and the same individual over the years (« longitudinal » studies). This lack of « longitudinal » information is however a serious limit to our full understanding of snake reproductive strategies (Madsen & Shine, 1992).

The recently emerged awareness of the relevance of the « longitudinal » approach for snake ecological studies has determined (i) a growing effort in such a field of research by snake biologists and (ii) the apparition of several relevant contributions on a few snake species, including adders *Vipera berus* (Andr n, 1982 ; Andr n & Nilson, 1983 ; Madsen & Shine, 1992, 1993, 1994 ; Capula & Luiselli, 1994 ; Luiselli, 1995), asps *V. aspis* (Bonnet & Naulleau, 1995 ; Saint Girons, 1996), Timber rattlesnakes *Crotalus horridus* (Martin, 1993), smooth snakes *Coronella austriaca* (Luiselli *et al.*, 1996a), and grass snakes *Natrix natrix* (Luiselli, 1996 ; Luiselli *et al.*, 1996b). All the above species are easily studiable because they are locally common, active above-ground and easily found in the field. However, due to the typically secretive habits of most snake species, there are still so many species that we know so little about. In fact, also in geographic

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regions traditionally « advanced » as far as the scientific research is concerned (e.g. western Europe or northern America), practically nothing is known on the year-by-year variations in reproductive performance of individuals of most snake species.

Amongst European snakes, the colubrid species belonging to the genus *Elaphe* are still largely unknown, and no « longitudinal » study is available. This lack of information depended not only on the very discrete habits of these snakes but also on the low population density typically exhibited by *Elaphe* species in most of their wide geographic range (for the case of Italy, see Filippi, 1995 ; Rugiero & Luiselli, 1996). With regard to the population ecology of the three species inhabiting the Italian peninsula, one is still completely unknown (*E. situla*), while « spotted » data on the other two species (*E. quatuorlineata* and *E. longissima*) is available but quite scarce indeed. To be more precise, data on the reproductive biology of the four-lined snake (*E. quatuorlineata*) is very poor either in nature (Rugiero & Luiselli, 1996) or in captivity (Pozio, 1976 ; Langeveld *et al.*, 1994). More information is available on the reproductive biology of the Aesculapian snake (*E. longissima*) (e.g. see Naulleau, 1992 ; Bonnet & Naulleau, 1994 ; Capula *et al.*, 1995a, Naulleau & Bonnet, 1995), but no specific study had a « longitudinal » approach.

Long-term field-work in the territory of Tolfa Mountains (province of Rome, central Italy) permitted us to obtain some remarkable data on the (1) frequency of reproduction, (2) reproductive output, (3) timing of egg laying, and (4) behaviours correlated with reproduction, in sympatric *E. quatuorlineata* and *E. longissima*. These data form the subject of the present paper. The present study is particularly relevant not only because it is the first in the world devoted to « longitudinally » monitor the reproductive outputs of *Elaphe* species, but also because it is one of the few studies that examine aspects of comparative reproductive ecology in sympatric *Elaphe*.

MATERIALS AND METHODS

STUDY AREA AND THE SPECIES

All data given here were collected in the territory of Tolfa Mountains, about 60 km north-west of Rome (about 150-300 m a.s.l., 42° 08' N latitude, 12° 00' east of Greenwich longitude). This territory is characterized by a complex sedimentary basement crossed and overlaid by eruptive rocks. The study area is characterized by a Mediterranean-temperate climate, with cold winter (without snow covering), rainy springtime and autumn, and dry and hot summer (hypomesaxeric subregion [type B] according to Tomaselli *et al.*, 1973). Mean monthly rainfall and mean monthly ambient (air) temperatures are given in Fig. 1. The total surface surveyed, about 150 ha, is characterized by three macrohabitat types available to snakes. Type (1), about 10 ha surface, is a riparian and wet forest phytocenosis (mainly *Ulmus campestris*, but also *Salix* spp. and *Populus* sp.) surrounding a stream called « Fosso Verginese » ; type (2), about 95 ha surface, are « bushy pastures », i.e. open grassy fields interspersed with bushes (*Spartium*, *Cytisus*, *Prunus*, *Rubus* and *Crataegus*) ; type (3), about 45 ha surface, is a mesophilous forest of *Quercus cerris*, *Ostrya carpinifolia* and *Quercus pubescens* (Spada, 1977).

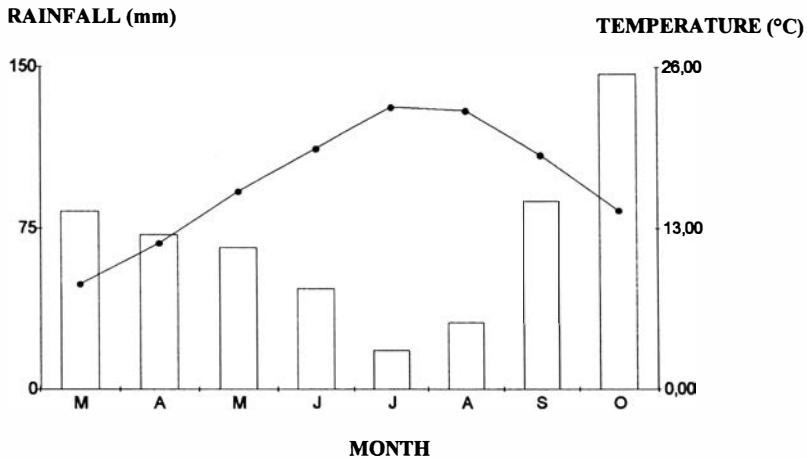


Figure 1. — Climatological data of the study area (Tolfa Mountains, Latium, central Italy). Mean monthly rainfall is represented by bars and mean monthly ambient (air) temperatures by lines. Data from the Meteorological Centre at Civitavecchia (Rome).

Both *E. longissima* and *E. quatuorlineata* are found in the study area. The former is quite common, especially in wet and forested areas (macrohabitat types (1) and (3)); the latter is rare, and found especially in macrohabitat type (2) (Filippi, 1995). Thus, although individuals of both species are occasionally found together (e.g. at basking during early springtime), the rule is that these two congeneric species partially subdivide the spatial niche (Filippi, 1995). Conversely, their diets (constituted by rodents and lizards) are very similar, although during springtime *E. quatuorlineata* tends to feed frequently upon birds and their nestlings (Cattaneo, 1979; Luiselli & Rugiero, 1993; Capizzi *et al.*, 1995; Capizzi & Luiselli, 1996).

METHODS

The study, conducted mainly from March 1990 to March 1996, is part of a larger research on the ecology and population biology of snakes in the territory of Tolfa Mountains (e.g. see Filippi, 1995, and references therein).

Standardized routes along the study area were done primarily during the morning hours (07 00-15 30), but field trips during late afternoon and night were also made.

When a snake was found, it was captured by hand, sexed by examining tail morphology, measured to total length (TL, to the nearest ± 0.5 cm) and weight (W, to the nearest ± 0.1 g), scale-clipped for future identification, and paint-marked with a white number in the dorsal parts for visual identification at distance. Paint-marking proved to work better during the dry season (summer months) than in springtime and autumn: in fact the white numbers remained well visible in the snake dorsal parts on average for over 40 days during summertime, but for less than 20 days during springtime or autumn. Since (i) all the eleven monitored

snakes were already large adults at the time of first capture, and (ii) growth rates in snake TL tend to decrease with age and increasing total length (e.g. see Luiselli *et al.*, 1996b), we avoided to re-measure their TLs over the years and assume that TL of every female remained constant throughout the study years (although some growth might have occurred). Whether the examined females had mated during the reproductive period was determined by examination of cloacal mucus (for the presence of spermatozoa) in the laboratory (Naulleau, 1992 ; Capula *et al.*, 1995c). The reproductive status of the females (gravid or nongravid) was determined by palpation of the abdomen and by considering the mass/length ratio (see Andr n & Nilson, 1983). Recaptures in successive years permitted to obtain data on the individual frequency of reproduction of females. Only females captured at least three successive years have been considered for this study (see also Capula & Luiselli, 1994). For every long-term monitored female we determined a frequency of reproduction index (FRR), defined as the ratio between number of years in which a given individual gave birth to young and total number of consecutive years in which it has been examined for reproductive status. If FRR equals to 0.5, this value indicates a biennial breeder, while if FRR equals to 1, this indicates an annual breeder (Capula & Luiselli, 1994).

Litter size was estimated by palpation of animal abdomen directly in the field. Strong logistic constraints (lack of enough space in the laboratory) impeded us to maintain in captivity the analysed females until egg laying occurred. Thus, some clutch parameters (e.g. offspring size, relative clutch mass, proportion of inviable eggs, etc.) were not recorded at all. However, previous field studies demonstrated that in *Elaphe* snakes egg-counts obtained by palpation were very close to egg-counts obtained after egg-laying of females housed in captivity until oviposition (Naulleau, 1992 ; Naulleau & Bonnet, 1995 ; Luiselli *et al.*, unpublished data).

Date, hour and air temperature of each spot of observation of snakes (in the closest point in the shade, at about 50 cm from the ground, by means of an high precision mercury thermometer) were also recorded.

STATISTICAL ANALYSES

Statistical analyses were done with both a STATISTICA per Windows (version 4.5, 1993) and a SPSS per Windows personal computer softwares. If not explicitly stated, all tests used were two-tailed, with α set at 5 %. All data were checked for homoscedasticity before selection of any test, and then normalized if necessary. When this procedure failed in obtaining a normal data distribution, non-parametric tests were used.

RESULTS

This « longitudinal » study is based on five females *E. longissima* and six females *E. quatuorlineata* monitored for at least three consecutive years (maximum obtained : six consecutive years in a female *E. quatuorlineata*). Many more specimens (44 *E. longissima* females and 29 *E. quatuorlineata* females) were marked during the six years of study, but disappeared and were thus unutilizable for this study.

FREQUENCY OF REPRODUCTION

In total we obtained 17 « snake-years » of records from females *E. longissima*, and 23 « snake-year » of records from female *E. quatuorlineata* (i.e. counting each female as a separate data point in each year she was collected). Females four-lined snakes were monitored on average for longer time than female Aesculapian snakes ($\bar{x} = 3.83 \pm 1.33$ versus 3.40 ± 0.55 years per female), but these timespans were not significantly different (differences between two-samples with *t* test, $df = 9$, $P = 0.51$).

The reproductive condition of each monitored snake year-by-year is shown in Table I. FRR averaged 0.817 ± 0.170 in *E. longissima* (variance = 0.029) and 0.893 ± 0.153 in *E. quatuorlineata* (variance : 0.023) (differences between two samples with *t* test, $df = 9$, $P = 0.455$), that means that in both species all the monitored females reproduced in most years. FRR ranged between 0.66 and 1 in both *E. longissima* and *E. quatuorlineata*. Two out of five (40 %) *E. longissima* and three out of six (50 %) *E. quatuorlineata* exhibited perfectly annual cycles, despite the sometimes very long timespan of study. Individual FRR was not significantly correlated with the number of consecutive years a snake was monitored ($r = 0.408$, adjusted $r^2 = 0.074$, $n = 11$, ANOVA : $F_{1,9} = 1.804$, $P > 0.21$), that means that the monitoring for very prolonged time of a female snake did not influence the probability to find her unproductive. No female of any species failed to reproduce for two consecutive years, contrary to what happens in other species from temperate zones (Capula & Luiselli, 1994 ; Luiselli *et al.*, 1996a).

FRR was strongly influenced by female body size in *E. longissima* but not in *E. quatuorlineata* : in fact, running the female TL (in cm) against FRR, a positive correlation was found in the former species ($r = 0.972$, adjusted $r^2 = 0.297$, $n = 5$, ANOVA : $F_{1,3} = 51.989$, $P > 0.0055$) but not in the latter one ($r = 0.518$, adjusted $r^2 = 0.855$, $n = 6$, ANOVA : $F_{1,4} = 1.467$, $P > 0.25$), and the difference between the regression lines relative to the two species was very close to the significance level (one-sided heterogeneity of slopes test : $P = 0.066$). Hence, our data on both *E. longissima* and *E. quatuorlineata* suggest that (i) most females are able to bear in most years, (ii) only in occasional cases a female fails to reproduce, and (iii) the bigger is the female, the more regular is the interval between two successive reproductive events (at least in *E. longissima*).

PROPORTIONS OF REPRODUCTIVE FEMALE SNAKES YEAR-BY-YEAR

Considering the two species together, the proportion of gravid females in each year ranged from 57 % (1992) to 100 % (1995), and averaged 81.6 ± 14.5 % (median = 84.3 %, variance = 21.2) throughout the whole study period (six years) (Fig. 2).

LITTER SIZE AND CLUTCH PARAMETERS

Data on litter sizes for the two studied species are given in Table I.

Clutch size averaged 9.43 ± 1.87 eggs in *E. longissima* (median = 9.5 eggs, range = 6/12 eggs, $n = 14$) and 10.22 ± 1.24 eggs in *E. quatuorlineata* (median = 10 eggs, range = 8/12 eggs, $n = 19$). These averages did not differ

PROPORTION BREEDING

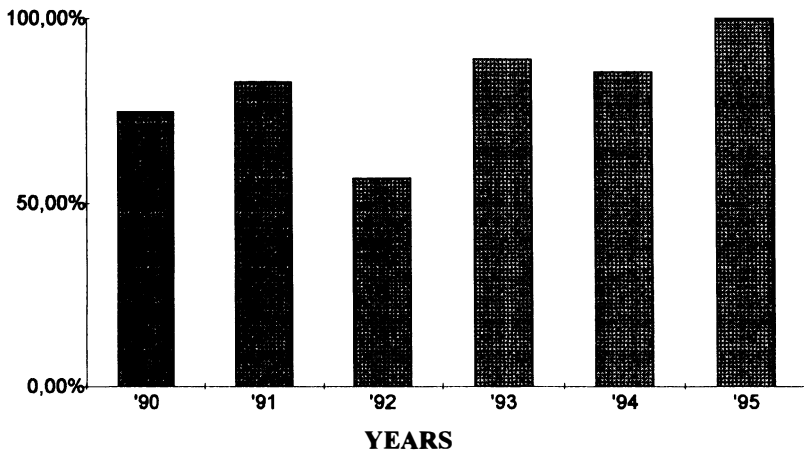


Figure 2. — Proportion of breeding females in each of the six study years. For statistical details, see text.

significantly (one-way ANOVA : $F = 1.07$, $P = 0.46$). The clutch size relative to female size averaged almost the same in both *E. longissima* ($\bar{x} = 0.08 \pm 0.01$, $n = 14$) and *E. quatuorlineata* ($\bar{x} = 0.07 \pm 0.01$, $n = 19$; differences between two samples insignificant at one-way ANOVA).

Considering all the « snake-years » of records as separate data-points, there was a positive linear correlation between female TL and litter size in both *E. longissima* ($r = 0.557$, adjusted $r^2 = 0.254$, $n = 14$, ANOVA : $F_{1,12} = 5.419$, $P > 0.038$) and *E. quatuorlineata* ($r = 0.645$, adjusted $r^2 = 0.382$, $n = 19$, ANOVA : $F_{1,17} = 12.123$, $P > 0.003$) (see Fig. 3). A two-sided heterogeneity of slopes test showed that the regression lines of clutch size versus maternal TL were not significantly different between species ($P = 0.727$). The total clutch produced by each female over the years (e.g., in the case of female *E. longissima* # 1, the complexive number of eggs produced in 1990, 1991 and 1993 [29 eggs]) was positively correlated (but not at a statistically significant level) with maternal TL in the case of *E. longissima* ($r = 0.827$, adjusted $r^2 = 0.578$, $n = 5$, ANOVA : $F_{1,3} = 6.487$, $P > 0.085$), while it was far from significance in the case of *E. quatuorlineata* ($r = 0.368$, adjusted $r^2 = 0.136$, $n = 6$, ANOVA : $F_{1,4} = 0.629$, $P > 0.045$).

Did some females produce larger litters than expected from their body sizes ? We examined this possibility by calculating residual scores from the general regression of litter size to maternal TL (Table I). A positive score means that a female produces a larger litter than expected from her TL, whereas a negative score means that her litter is smaller than expected from her TL. Data analysis suggests that *E. quatuorlineata* females were consistent in relative fecundity across years (one-factor ANOVA with maternal identity as the factor and the residual fecundity score as the dependent variable : $P < 0.02$), whereas *E. longissima* females were not (one-factor ANOVA : $P > 0.35$).

TABLE I

Reproductive condition of female Elaphe longissima and E. quatuorlineata, monitored over several years at the study area. « NP » means non-pregnant status; « TL » indicates the female length (in cm); numbers indicate the litter size of each female in each year, and the numbers in parentheses indicate the residual fecundity score calculated from the general regression of litter size to maternal length.

Individual TL		Years					
		1990	1991	1992	1993	1994	1995
<i>E. longissima</i>							
# 1	117	9 (0.179)	9 (0.179)	NP	11 (2.179)		
# 2	129	10 (- 0.644)	11 (0.356)	8 (- 2.644)			
# 3	111		NP	6 (- 1.908)	7 (- 0.908)		
# 4	126			8 (1.811)	12 (0.811)	12 (0.811)	11 (- 2.188)
# 5	115				NP	8 (- 0.517)	10 (1.483)
<i>E. quatuorlineata</i>							
# 1	143	9 (- 0.732)	10 (0.267)	8 (- 1.732)			
# 2	140		9 (- 0.508)	NP	10 (0.492)	10 (0.492)	11 (1.492)
# 3	154	NP	11 (0.444)	NP	11 (0.444)	10 (0.444)	12 (1.444)
# 4	166				12 (0.545)	12 (0.545)	12 (0.545)
# 5	162				10 (- 1.155)	10 (- 1.155)	10 (- 1.155)
# 6	138				8 (- 1.358)	NP	10 (0.642)

Detrended normal probability plots of residual scores running against deviations from expected values are shown in Figure 4. Fecundity residuals from the general regression of litter size to maternal TL were not significantly correlated with the proportion of breeding females per year neither if we consider the two species separately or together (together : $r = 0.199$, adjusted $r^2 = 0.088$, $n = 33$, ANOVA : $F_{1,31} = 1.284$, $P > 0.25$). Moreover, there was no significant association between negative (or positive) fecundity residual scores and the year of study ($P > 0.35$), that means that no study year was particularly positive (or negative) for the production by all the examined females of larger (smaller) litters than expected from their body sizes.

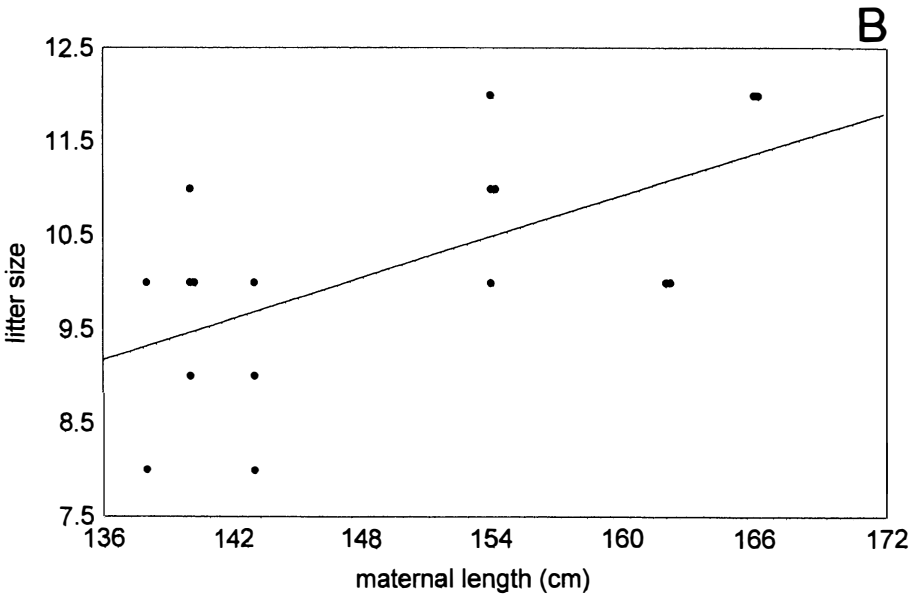
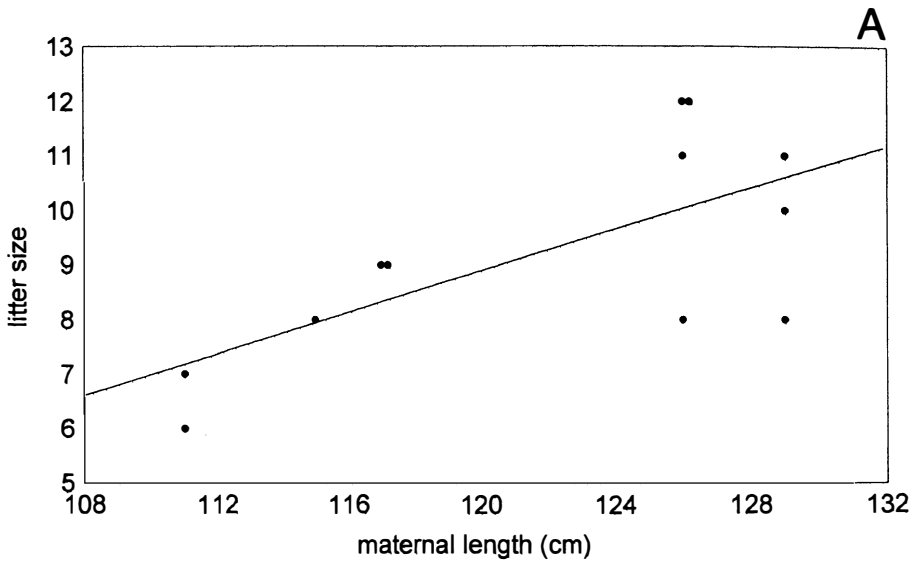


Figure 3. — Relationships between female length (TL, in cm) and clutch size in sympatric *Elaphe* from the study area. A : *E. longissima* (regression equation — Litter size = - 8.959 + 0.15196 * Maternal length) ; B : *E. quatuorlineata* (regression equation — Litter size = - 0.9736 + 0.7487 * Maternal length).

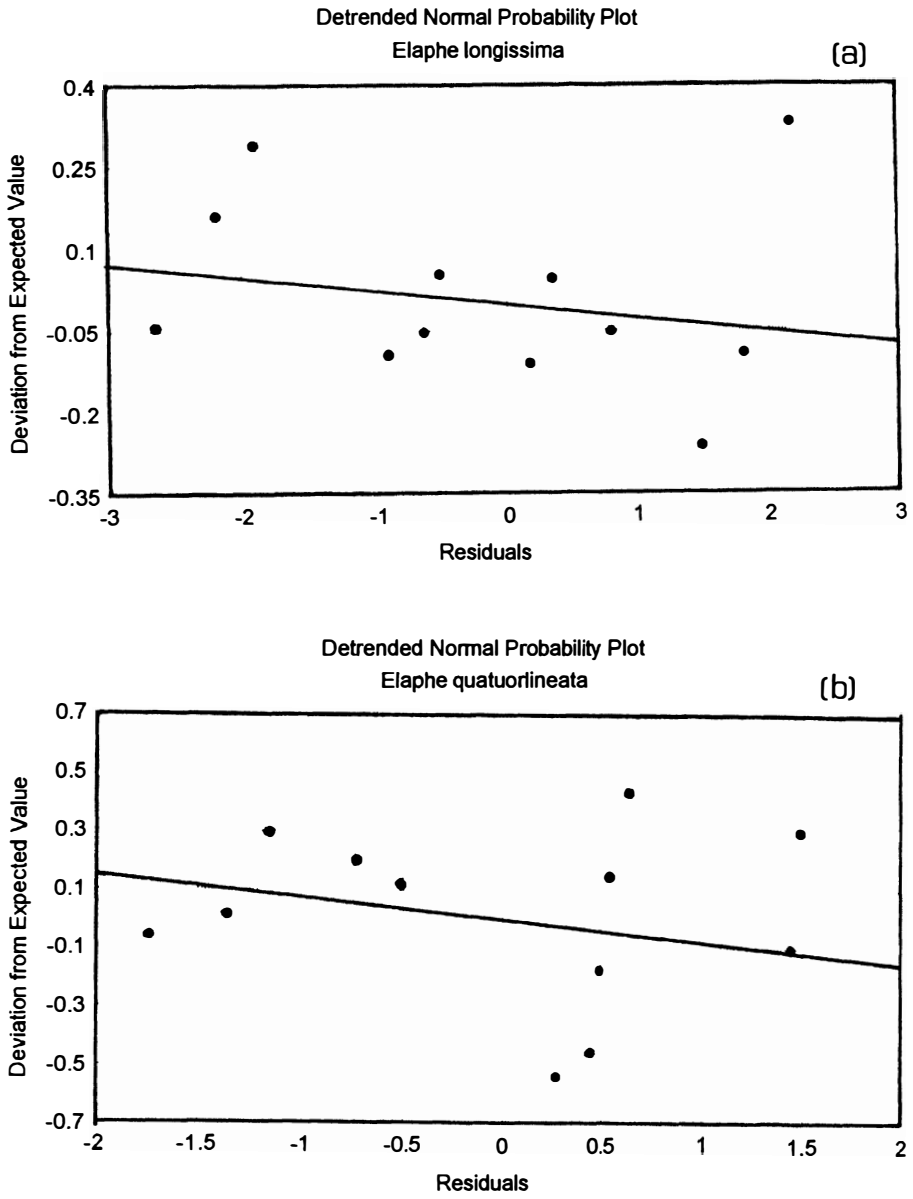


Figure 4. — Detrended normal probability plot of fecundity score residuals calculated from the general regression of litter size to maternal length (TL, in cm) in sympatric *Elaphe* from the study area. A : *E. longissima* ; B : *E. quatuorlineata*.

TIMING OF OVIPOSITION

Timing of egg deposition was determined by palpation of the females recaptured more than once during June-July. We determined (with reasonably good approximation) the date of oviposition of 11 females *E. longissima* and 9 females *E. quatuorlineata* from the study area (including also a few specimens that were not monitored over the years and that are not included in the analyses at above).

Oviposition dates were consistent between the species and between the years: they always occurred between 19th July and 2nd August. However, our data are too scarce for determining whether some correlation between maternal size and oviposition date could exist (for the cases of *C. austriaca* and *N. natrix*, see Luiselli *et al.*, 1996a, 1996b). Hatching occurred in both taxa at the end of August (Filippi, 1995).

« AFTER-LAYING » MORTALITY COSTS

We had firm evidence of female mortality after-laying eggs in one case only, relative to *E. longissima* individual # 3 (in Table I). She was found dead on 7th August 1993, i.e. about ten days after laying eggs (this specimen is now stored in the private collection of LL). Autopsy revealed neither apparent diseases nor predation marks, thus permitting us to conclude that, given its very poor BCI (*sensu* Bonnet & Naulleau, 1994), the most probable cause of death could be the high degree of emaciation. In all the other cases the reproductive females survived to the parturition event without revealing major problems. Thus, mortality costs associated with reproduction could be low in both the species studied here.

BEHAVIOURAL TRAITS ASSOCIATED WITH REPRODUCTION

In outdoor enclosure the gravid females of both *E. longissima* and *E. quatuorlineata* spent more time in thermoregulation than males and juveniles (Trujillo Jesus *et al.*, unpublished work). However, this basking rate increasing is difficult to be revealed by field observations, although it likely occurs also among free-ranging individuals. Our field observations suggest that gravid females (i) usually use dry substratums (wood-piles and dried leaves) for thermoregulation, and (ii) normally avoid to remain fully exposed to sun when basking, but maintain part of their body in the shade or covered into bushes. It might be suggested that this latter basking behaviour is important not only in terms of optimization of thermal requirements but also in terms of reduction of predation risks.

In five different times (three relative to *E. quatuorlineata* and two to *E. longissima*) the gravid females were seen motionless in the water of small ponds along the banks of the stream « Verginese ». They remained in water for prolonged time (12 to 43 minutes), always during the hottest daily hours (12 26-14 55 in European Standard Time). This behaviour was never mentioned in earlier studies on *Elaphe* species, but it is curious that *E. quatuorlineata* are well known for spending many hours inactive in the water when housed in captivity, especially during specific phases such as moulting periods and digestion periods (Pozio, 1976; Luiselli *et al.*, unpublished work).

DISCUSSION

PATTERNS OF REPRODUCTIVE TRAITS IN SYMPATRIC *ELAPHE*

Despite the small number of monitored individuals, this long-term study permitted to obtain detailed information on the reproductive habits of sympatric *Elaphe* in Mediterranean ecosystems of central Italy.

To begin with, four-lined snake females were captured for longer timespans than Aesculapian snake females, but the interspecific differences did not attain statistical significance (probably due to the very small number of animals examined). Actually we cannot know whether this difference between species depended on different catchability (i.e. one species more elusive than the other), different survival rates (i.e. one species more longeval than the other), or different homing strategies (i.e. one species less mobile than the other).

In both species most females were able to bear once per year. This trend is consistent with other datasets available for oviparous colubrids in temperate regions : in fact, either cross-sectional or longitudinal studies show that western European oviparous colubrids are normally able to bear once per year not only in mild climate areas (e.g. Mediterranean, see Agrimi & Luiselli, 1994 ; Filippi, 1995), but also in mountainous areas with cold winters and prolonged snow covering (Luiselli *et al.*, 1996b).

Considering the *E. longissima* « snake-years » of records, we conclude that about 82 % of the adult females are able to bear every year. This proportion is very similar to that of conspecifics from western France. In this region about 16 % of the potentially breeding females are in fact unable to bear in each year (Naulleau, 1992). This strong similarity between snake populations inhabiting climatically different areas is intriguing, as female snake proportion breeding tends to lower with latitude or altitude increases, chiefly with ambient temperature lowering (e.g. see Saint Girons, 1952, 1957, and later studies). According to Naulleau & Bonnet (1995), the high breeding proportion of *E. longissima* females (in comparison with sympatric live-bearing snakes such as *V. aspis*) is due to the fact that, after laying, the mean body condition index is close to the reproductive threshold value, so that it is relatively easy to reach the reproductive threshold again after only a few months of predatory activity. In this regard, it is obvious that the eclectic and opportunist predatory habits of this snake (see Capizzi *et al.*, 1995) could further facilitate the body reserve reconstruction within short timespans. With regard to *E. quatuorlineata*, given its relative foraging opportunism (Capizzi *et al.*, 1995), the situation is likely to be similar, but no data are available on the tradeoffs between feeding ecology and reproductive output in this species.

The two *Elaphe* species clearly differed in the fact that FRR increases with body length (i.e. age) in one species (*E. longissima*) but not in the other (*E. quatuorlineata*). FRR increases with age in *Coronella austriaca* (Luiselli *et al.*, 1996a), *Vipera aspis* (Saint Girons, 1996), *Vipera ursinii* (Baron *et al.*, 1996), and *Crotalus horridus* (Martin, 1993), but not in *Vipera berus* (Capula & Luiselli, 1994).

The interannual variations in (i) breeding proportion, (ii) individual fecundity, and (iii) residual scores from the general regression of litter size to maternal TL, were insignificant in both species. Lack of significance in the interannual variations of the above parameters has already been observed in snake populations inhabiting areas with abundant or unfluctuating food resource (e.g. see Capula *et al.*, 1992 ; Luiselli *et al.*, 1996a, 1996b), whilst snake reproductive performances (and correlated behaviours) significantly vary amongst years in areas with fluctuating food resources (Andr n, 1982 ; Andr n & Nilson, 1983). Although we have no data on the population dynamics of small mammals — main prey for both *Elaphe* species : see Luiselli & Rugiero, 1993 ; Capizzi *et al.*, 1995 — in the study

area, it is likely that their interannual fluctuations are scarce, thus following a general pattern for small mammal populations in the Mediterranean ecosystems.

Examination of reproductive output and timing of egg laying revealed remarkable consistency between the two *Elaphe* species : in fact (i) dates of egg laying, and (ii) clutch size relative to maternal size were nearly identical in the two taxa. Moreover, an heterogeneity of slopes test showed a remarkable similarity between species in the (positive) relationship between clutch size and maternal TL.

Our study also revealed some interspecific differences between sympatric *Elaphe*. The most interesting one was in the degree of consistency in reproductive output by a given female in successive clutches. In fact, whereas in one species (*E. longissima*) this consistency was minor, in the other species (*E. quatuorlineata*) most of the females tended to be consistent in terms of litter size throughout years. Very few are the studies that investigated consistency in reproductive traits of female snakes in successive clutches. Alpine grass snakes (*N. natrix*) proved to be not consistent in terms of several reproductive traits (including clutch size) but in terms of (i) the body shape of their hatchlings, (ii) the degree of female emaciation after oviposition and (iii) the incubation periods (Luiselli *et al.*, 1996b). Alpine smooth snakes (*C. austriaca*) were not consistent in terms of most traits, including litter size (Luiselli *et al.*, 1996a), whereas Australian water pythons (*Liasis fuscus*) were consistent in most of these traits (Madsen & Shine, 1996). The significance of the different « litter size consistency » pattern observed in the two studied *Elaphe* remains obscure, but is intriguing and merits further investigation.

The experimental design of our long-term research did not focus on studying the costs of reproduction of these snake populations as earlier researches did (e.g. see Luiselli, 1992 and Madsen & Shine, 1993 for *V. berus* ; Luiselli *et al.*, 1996a for *C. austriaca* and Luiselli *et al.*, 1996b for *N. natrix*). The essential parameter we did not measure was RCM (Relative Clutch Mass), that may offer a convenient and operationally simple measure that broadly integrates costs in different currencies (energy and risk, e.g. see Luiselli *et al.*, 1996b). However, two main aspects of the reproductive traits of both the studied species — i.e. (i) the mostly annual frequency of reproduction and (ii) the evidence of low mortality rates after laying eggs — suggest that mortality costs after-laying should probably be low in *Elaphe* populations from Mediterranean ecosystems, contrary to what appears true for snake populations of colder regions (e.g. see Luiselli, 1992 ; Madsen & Shine, 1993 ; Luiselli *et al.*, 1996a, 1996b). Mortality costs associated with reproduction could perhaps be higher in areas inhabited by raptors specialized in feeding upon snakes (e.g. the Short-toed Eagle, *Circaetus gallicus*). These raptors are in fact well known for preying frequently upon *Elaphe* and *Coluber* individuals rather than upon venomous vipers (Bruno & Perco, 1981 ; Petretti, 1988). At our study area, however, *Circaetus gallicus* is extremely rare (F. Angelici, personal communication) and thus cannot be considered as an hard predatory risk for our female snakes.

COMPARISONS WITH OTHER CONGENERIC POPULATIONS

No doubt the data given here are the most detailed available on reproductive output of *E. quatuorlineata* in the field. Thus, comparisons with other conspecific

populations are difficult due to the scarcity of the available data. However, the mean clutch size of the four-lined snakes studied here was very similar to that of another conspecific population studied by Rugiero & Luiselli (1996) in Mediterranean central Italy ($\bar{x} = 10.83 \pm 1.17$ eggs, $n = 6$; differences between populations : $P = 0.386$ at two-tailed Student t test).

With regard to *E. longissima*, the mean clutch size of the population studied here was significantly higher than that recorded by Naulleau (1992) in central-western France ($\bar{x} = 6.7 \pm 1.75$ eggs, $n = 20$; differences between populations : $P = 0.0002$ at two-tailed Student t test). This difference was clearly due to the significantly longer TL attained by the Italian snakes (means = 119.6 cm versus 101.11 cm), as the clutch size relative to female size (calculated from Fig. 3 in Naulleau, 1992 as for the French population is concerned) averaged similar in both localities (Student t test, $P > 0.4$). It is unfortunate that, since no data on female age are actually available for any of these populations, we cannot evaluate whether the different mean body sizes depended on older mean age or increased growth rates (due to milder climatic conditions) of the Italian versus the French females.

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SUMMARY

Reproductive status, litter size, and correlated behaviours have been studied in a few long-term monitored females of the sympatric snakes *Elaphe quatuorlineata* ($n = 6$) and *E. longissima* ($n = 5$). The study was carried out in a hilly territory of Mediterranean central Italy (Tolfa Mountains, Latium). This study revealed that both species were similar in terms of frequency of reproduction (most females were able to bear in most years), absolute clutch size (9.42 ± 1.86 eggs in *E. longissima* and 10.32 ± 1.25 eggs in *E. quatuorlineata*), clutch size relative to maternal size (0.08 ± 0.01 in *E. longissima* and 0.07 ± 0.01 in *E. quatuorlineata*), timing of egg laying (from 19th July to 2nd August) and timing of egg hatching (late August). Moreover, there was evidence of low mortality costs associated with post-oviposition in either species. *E. quatuorlineata* females were consistent among years in the litter size they produced, while the same was not true for *E. longissima* females. No study year was particularly positive (or negative) for the production by all the examined females of larger (smaller) litters than expected from their body sizes.

RÉSUMÉ

Le statut reproducteur, la taille des portées et les comportements liés à ces paramètres ont été étudiés par suivi sur le long terme de femelles de deux espèces

de couleuvres sympatriques *Elaphe quatuorlineata* ($n = 6$) et *E. longissima* ($n = 5$). L'étude a été conduite dans une zone de collines méditerranéennes du centre de l'Italie (Monts de Tolfa, Latium). Elle a révélé que les deux espèces sont semblables en termes de fréquence de la reproduction (la plupart des femelles portent chaque année), de taille absolue des pontes ($9,42 \pm 1,86$ œufs pour *E. longissima* et $10,32 \pm 1,25$ œufs pour *E. quatuorlineata*), de taille de la ponte relativement à celle de la femelle ($0,08 \pm 0,01$ chez *E. longissima* et $0,07 \pm 0,01$ chez *E. quatuorlineata*), de période de ponte (du 19 juillet au 2 août) et de période d'éclosion (fin août). De plus, sont apparus chez les deux espèces de faibles coûts de mortalité associés à la post-oviposition. Les femelles d'*E. quatuorlineata* ont toutefois produit, d'année en année, des portées de même taille, ce qui ne fut pas le cas de celles d'*E. longissima*. Aucune des années de l'étude ne fut particulièrement positive (ou négative) pour ce qui concerne la production par toutes les femelles examinées de portées plus importantes (ou plus faibles) que celles attendues de leur taille corporelle.

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