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A tentative review of sexual behavior and alternative reproductive strategies of the Italian colubrid snakes
(Squamata: Serpentes: Colubridae)

Versuch einer Zusammenschau über das Sexualverhalten und alternative Fortpflanzungsstrategien der Nattern Italiens
(Squamata: Serpentes: Colubridae)

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KURZFASSUNG

Die vorliegende Arbeit gibt einen Überblick über das Fortpflanzungsverhalten der Nattern Italiens unter besonderer Berücksichtigung von Männchen-Männchen-Kämpfen um den Zugang zu fortpflanzungsfähigen Weibchen sowie von alternativen Fortpflanzungsstrategien. Wir diskutieren (i) die verfügbaren Literaturdaten, stellen (ii) Originaldaten über wenig bekannte Arten vor und machen (iii) den Versuch einer vorläufigen Typisierung dieser Kämpfe zwischen männlichen Colubriden Italiens. Danach lassen sich vier Typen von Kämpfen unterscheiden, wobei Beißen nur bei ungiftigen Schlangen vorkommt. Die Kämpfe führen in der Regel nicht zur Beschädigung der Beteiligten, doch wird für *Elaphe situla* ein Fall mit fatalem Ausgang berichtet. Kämpfe zwischen Männchen wurden bei 13 der 19 Schlangenarten Italiens (68,4%) festgestellt und bisher an 21 Populationen untersucht. Diese Prozentangabe ist wahrscheinlich korrekturbedürftig, da Angaben zu drei sehr seltenen Arten nicht verfügbar sind. Nur bei der Gattung *Natrix* scheinen Kommentkämpfe nicht vorzukommen, doch könnten bei *N. natrix* physische Interaktionen zwischen Männchen, die gleichzeitig um ein einzelnes Weibchen werben, zu einer Art "Pseudokampf" führen, in dem die Größe des Männchens für seinen individuellen Fortpflanzungserfolg bedeutsam sein kann. Im Dienste der Fortpflanzung stehende Kämpfe fanden sich bei Schlangenarten, in denen die Männchen größer sind als die Weibchen (n = 5), ebenso wie bei Arten ohne ausgeprägten sexuellen Größendimorphismus (n = 4) und bei Arten mit größeren Weibchen (n = 4). Die Analyse zeigt einen Zusammenhang zwischen Sexualdimorphismus mit größeren Männchen und dem Auftreten von Kämpfen sowohl bei den Colubriden Italiens als auch bei Schlangen im allgemeinen (SHINE 1978, 1993, 1994). Kämpfe ließen sich bei 100% der lebendgebärenden Taxa (inklusive Viperiden: n = 5 Arten), jedoch nur bei 72,7% der oviparen Formen nachweisen. Bei einigen Arten zeigten sowohl alpine als auch mediterrane Populationen diese sozialen Verhaltensweisen. Herbstpaarungen, Frühjahrsgeburten und Langzeit-Samenspeicherung wurden bei den Nattern Italiens nur selten beobachtet.

ABSTRACT

In this paper data on the reproductive behavior of the Italian colubrid snakes are reviewed, with an emphasis on the occurrence of male-male combats for the access to reproductive females, and on the occurrence of alternative reproductive strategies. We (i) discuss the data available in the literature, (ii) include original information on the most unknown species, and (iii) give a tentative "classification" of the behavioral types of male combats exhibited by the colubrids of the Italian Peninsula. Four types of sexual combats were identified, but biting is present only in non-venomous species. Combats were generally harmless to the rivals, but a case of fatal combat is reported for *Elaphe situla*. Sexual fights among males were seen in 13 out of the 19 Italian snake species (68.4%), and studied in 21 different populations to date. This proportion should probably be retouched as we had no available information on three very rare species. The sole taxa that seem to lack sexual fights are those of the genus *Natrix*, but in *N. natrix* some physical interactions between males simultaneously courting single females may lead to a kind of "pseudocombat" where male body size is important for increasing the individual reproductive success. Sexual combats were found in snake species where males are bigger than females ($n = 5$), in species with no significant sexual size dimorphism ($n = 4$), and in species with females bigger than males ($n = 4$), but, examining the data in more detail, it turned out that male-larger dimorphism and occurrence of sexual combats are correlated in Italian colubrids, as well as in snakes in general (SHINE 1978, 1993, 1994). Sexual combats were omnipresent in the live-bearing taxa (vipers included: $n = 5$ species, 100% of the cases), but were present in 72.7 % of the oviparous ones. In some species these social behaviors were exhibited both by alpine and Mediterranean populations. Autumnal mating, spring births, and long-term sperm storage were rarely observed amongst Italian colubrids.

KEY WORDS

Serpentes, Colubridae; *Natrix maura, N. natrix, N. tessellata, Coluber gemonensis, C. viridiflavus, Coronella austriaca, C. girondica, Elaphe longissima, E. quatuorlineata, E. scalaris, E. situla, Macroprotodon cucullatus, Malpolon monspessulanus, Telescopus fallax;* behavior, reproductive biology, sexual competition, combats, alternative mating strategies, long term sperm storage, autumnal mating, spring births; Italy.

INTRODUCTION

In recent years the available data on snake reproductive biology and mating systems has expanded enormously, and the comparative analysis of this large databody has produced vigorous improvement in our knowledge (e.g., SHINE 1978, 1994). For instance, it is now clear that male-male combats are important components of the reproductive biology of many snake species, while less than twenty years ago these agonistic behaviors were known in 5.5% of the genera and in less than 2% of the known species only (CARPENTER 1977a).

The secretive habits of most snakes cause strong constraints to field research (SEIGEL 1993), and this has resulted in that we only know in detail the components of the reproductive biology of a few (less secretive or very common) species, while there are still so many species that we know very little about. As for the European species, a large body of eco-ethological studies is available for species such as the Adder *Vipera berus* (for a recent review see LUISELLI 1995), Smooth Snake *Coronella austriaca* (SPELLERBERG & PHELPS 1977; GODDARD 1981; GENT 1988; ANDRÉN & NILSON 1992; LARSSON 1994; LUISELLI & al. 1996) and Grass Snake *Natrix natrix* (e. g., MADSEN 1983, 1984, 1987; MADSEN & SHINE 1993a, 1993b; LUISELLI 1996; LUISELLI & al., 1997), while the information on other widespread taxa (e. g., *Elaphe situla*, *Telescopus fallax*, *Coluber viridiflavus*) is very sparse and anecdotal. This disproportionate knowledge is clearly expressed by some recent reviews of snake behavioral biology, such as those of SHINE (1993, 1994). In his exhaustive reviews on sexual dimorphism and male combats in snakes, SHINE collated data from 374 taxa of eight families, but scarcely presented the European forms. This becomes evident when we examine the snake fauna of the Italian Peninsula: although it includes 19 species from two families (4 viperids and 15 colubrids), SHINE (1994) was only able to list 9 species (47.3% of the total), but none of the papers reviewed by him was specifically concerned with Italian populations of snakes. However, several Italian snake populations have been subject to accurate field-research in recent years (e. g., CIOFI & CHELAZZI 1991, 1994; CAPULA & LUISELLI 1994; LUISELLI 1995, 1996).

Aim of this paper is to collate data on the reproductive behavior of the Italian colubrid snakes, focusing on male combats and alternative mating strategies. We discuss the data available in the literature, but also include original information on the most unknown species. Our attention has been focused on (1) the occurrence of male-male combats for access to females and its relation to sexual size dimorphism and operational sex-ratio; (2) the main characteristics of reproductive phenology (e. g., duration of mating season etc.); and (3) the potential for long-term sperm storage and other alternative reproductive strategies to occur. We also give a tentative "classification" of the behavioral types of male combats exhibited by the snakes of the Italian Peninsula. In order to highlight all of these points, we will systematically account on every colubrid snake species of the Italian fauna.

MATERIALS AND METHODS

The data presented here comes from both literature papers and original observations. The latter were done both in captivity and in the field, especially in two regions where long-term researches on snake behavior have been conducted: (i) a Mediterranean hilly site in central Italy - Tolfa Mountains, province of Rome, and (ii) an alpine mountainous site in northeastern Italy - Tarvisio Forest, Carnic Alps, province of Udine. The sources of all observations are presented in table 1. In the following text the term "sexual size dimorphism" is abbreviated by SSD.

To give a preliminary "classification" of the behavioral types of male combats exhibited by the snakes of the Italian Peninsula, we subdivide male combats into four groups: type (1): highly ritualized dances without biting (*Vipera* type, see SAINT GIRONS 1947; ANDRÉN 1986); type (2): combats based on vigorous biting (as in

many *Lampropeltis*, see CARPENTER 1986); type (3): combats based on both vigorous biting and tail wrestling (as in *Coronella girondica*; see below); type (4): combats ritualized with occasional biting. This classification is merely tentative, as (i) it is very difficult to observe the sexual combats from beginning to the end of the interaction in nature, (ii) terrarium experiments may be not representative of the natural situation, and (iii) the quantitative description of the agonistic behaviors needs to be very accurate (for excellent examples see ANDRÉN 1986; SCHUETT & GILLINGHAM 1989), and goes much beyond the scope of this article.

RESULTS

The knowledge on the reproductive biology and behavior of the Italian colubrids is generally less than that of the Italian vipers. This is due to (1) the obvious argument that venomous snakes capture the attention of scientists more than the non-venomous ones, (2) the more secretive habits of most colubrids in comparison with the viperids, (3) the lower site-fidelity of the colubrids which causes strong problems to field research, and (4) the low density of most colubrid populations at the very local scale which is not ideal for field studies.

At an extremely detailed level we know the reproductive biology of one alpine population of *Coronella austriaca* (LUISELLI & al. 1996) and of both alpine and Mediterranean populations of *Natrix natrix* (LUISELLI 1996a; LUISELLI & al. 1997). The reproductive behaviors of the other species are less well known, and the available data is very poor.

Male-male competition and mating behavior: A systematic account

The data on the occurrence of male-male competition, body sizes of the two sexes, and reproductive mode is summarized in table 1.

Natrix: Three species belonging to this genus are found in Italy; all are oviparous, semi-aquatic, and with female-larger SSD. Coloration of males and females is nearly identical in each species.

Grass Snakes - *Natrix natrix* (LINNAEUS, 1758) are known for frequently forming "mating balls" during the reproductive season (BRUNO & MAUGERI 1990; MADSEN & SHINE 1993a). When several males simultaneously court one female, their tails frequently and vigorously interact with each others, and the larger individuals often drive away the tails of the smaller rivals (MADSEN & SHINE 1993a; LUISELLI 1996). These "electric" gregarious courtships may last for a very variable time (sometimes for more than one hour) until one of the males becomes able to insert a hemipenis into the female cloaca; the female, however, is not passive in this context (LUISELLI 1996). Immediately after the beginning of the successful copulation, the other males in the swarm continue to "electrically" move around the copulating pair, thus disturbing the action of the mating couple by a series of tail and body movements. If the mating pair continues copulation despite the other males disturbance, the sexual agitation of the other males begins to decrease, and the copulating pair is usually abandoned within some minutes (MADSEN & SHINE 1993a; LUISELLI 1996).

In the eastern Alps (Tarvisio Forest, province of Udine, about 1100 m a.s.l), the mating season is short (2-3 weeks on average, from mid-May to early June) and explosive: since not all the females emerge from hibernation on the same day, the daily operational sex-ratio is strongly skewed to males (which emerge from hibernation earlier than the females), so that it is easy to see four or five individuals simultaneously courting a single female (LUISELLI & al. 1997). In Mediterranean central Italy (Tolfa Mountains, province of Rome, about 250-450 m a.s.l) the operational sex-ratio is equally skewed, but the mating season is much more prolonged (at least 5 weeks), and as a consequence, the mating "balls" are usually formed by a lower number of

Table 1: Occurrence of sexual combats, sexual size dimorphism and mode of reproduction in various populations of Italian snakes according to literature and original data. Information from only Italian populations is given.

Types of combat: 1: ritualized dance without biting (*Vipera berus* type); 2: combat based on vigorous biting; 3: combat based on vigorous biting and tail wrestling; 4: combat ritualized with occasional biting. Mean adult total lengths (TL) are given for males and females (m / f) and are expressed in cm. When total lengths were not available from literature, the approximate averages found by us during our field trips are given. Some species appear more than once because data are available from more than one source. The symbol (!) indicates our unpublished observations. When the observations are original, the geographic position and the climate of the area where these data were obtained are given.

Tab 1: Auftreten von paarungsbedingten Kämpfen zwischen Männchen und sexuellem Größendimorphismus sowie Fortpflanzungsmodus in verschiedenen Schlangenpopulationen Italiens auf Grundlage von Literaturangaben und Originaldaten. Angaben beziehen sich nur auf italienische Populationen.

Typisierung der Kämpfe: 1: Ritualisierter Tanz ohne Beißen (*Vipera berus* Typ); 2: Kampf mit heftigem Beißen; 3: Kampf mit heftigem Beißen und Ringen; 4: Ritualisierter Kampf mit gelegentlichem Beißen. Mittlere Gesamtlängen (GL) von adulten Männchen und Weibchen (m / w) sind in cm angegeben. Wo solche Längen aus der Literatur nicht verfügbar waren, wurden entsprechende Werte aus unseren Felduntersuchungen angegeben. Arten erscheinen mehrmals in der Tabelle wenn Daten aus mehr als einer Quelle verfügbar waren.. Ein Rufzeichen (!) bezeichnet eigene unpublizierte Angaben. Bei solchen Originalangaben ist die geographische Lage angegeben und das Klima des Untersuchungsgebietes charakterisiert.

A - [Tolfa Mountains, about 300 m a.s.l., Mediterranean climate], B - [Carnic Alps, about 1100 m a.s.l., alpine climate], C - [observations on captive animals from Croatian coast, about 20 m a.s.l.], D - [Central Apennines, about 800 m a.s.l., Subcontinental climate], E - [Roman Country, 100 m a.s.l., Mediterranean climate], F - [central and southern Italy, Mediterranean climate], G - [Salento, about 50 m a.s.l., Mediterranean climate], H - [observations in captivity from animals of Lampedusa, Mediterranean climate].

Species Art	Combat Kampf	Type Typ	Reprod. mode Reprod.-modus	Mean TL (m / f) Mittlere GL (m / w)	Locality Ort	Reference Quelle
Natrix maura	no	-	ovip.	45.5 / 55.5		BRUNO (1984)
Natrix natrix	no	-	ovip.	84.3 / 99.7	A	LUISELLI (1996)
Natrix natrix	no	-	ovip.	68.5 / 82.5	B	(!)
Natrix tessellata	no	-	ovip.	62.2 / 78.5	A	FILIPPI (1995)
Coluber hippocrepis	?	?	ovip.	115 / 90		–
Coluber gemonensis	yes	1	ovip.	110 / 90	C	(!)
Coluber viridiflavus	yes	1	ovip.	125 / 105	A	(!)
Coluber viridiflavus	yes	1	ovip.	121 / 117	D	(!)
Coronella austriaca	yes	2	vivip.	51.1 / 48.7	B	(!)
Coronella girondica	yes	3	ovip.	52.4 / 50.8	A	(!)
Elaphe longissima	yes	1	ovip.	110.3 / 106.5	A	(!)
Elaphe longissima	yes	1	ovip.	116 / 102	E	(!)
Elaphe quatuorlineata	yes	?	ovip.	? / ?	F	POZIO (1976)
Elaphe quatuorlineata	yes	4	ovip.	130 / 155	A	(!)
Elaphe situla	yes	4	ovip.	70 / 90	G	(!)
Elaphe scalaris	?	?	ovip.	85 / 120		–
Macroprotodon cucullatus	yes	2	ovip.	45 / 45	H	(!)
Malpolon monspessulanus	yes	1	ovip.	130 / 90		FRETEY (1987)
Telescopus fallax	?	?	ovip.	70 / 80		–

animals than in the Alps or in northern Europe (LUISELLI 1996). True combats between males were never observed by us. However, studies on Grass Snakes (*N. natrix*) held in both captivity (MADSEN & SHINE 1993a) and semi-natural conditions (LUISELLI 1996) suggest that in these "mating balls" the larger males copulate more frequently than the smaller ones because they are more vigorous and thus more able to obtain a good position for copulating. The age of the fighting males was not correlated with individual mating success both in the field and in outdoor enclosures (LUISELLI 1996). LUISELLI (1996) demonstrated that larger females attracted more males than smaller ones, probably because of size-dependent differences in sexual pheromone production.

No comparably detailed data is available for *N. maura* (LINNAEUS, 1758) and *N. tessellata* (LAURENTI, 1768). Observations on *N. tessellata* in the Tolfa Mountains (central Italy) suggest that courtship by multiple males (2-5 per female) occurs frequently in water: the males, usually smaller than their partner (FILIPPI & al. 1996; ZIMMERMANN & FACHBACH 1996), swim around the female trying to insert their hemipenis into 'her' cloaca. Copulation oc-

curs when the female stops swimming, and rests almost motionless on an emerging islet or on submerged grounds. Eventual determinants of individual reproductive success are completely unknown in both species, yet concerning *N. tessellata* experimental research started in 1995. In the Tolfa Mountains *N. tessellata* does not show an explosive mating season, and mating "balls" are less frequently found than in *N. natrix*.

Coluber: Three species belonging to this genus are found in Italy; all are oviparous and with male-larger SSD. There is no obvious chromatic sexual dimorphism in any of the Italian species of this genus.

The reproductive behavior of *C. gemonensis* LAURENTI, 1768 is completely unknown, because of its rarity in the Italian territory (LAPINI 1983). Ritualized combats between two Croatian males housed in captivity by us were frequently observed during April 1995. These males had a total length of 106 cm and 101.5 cm, respectively. Their combats occurred also for food when dead lizards or mice were put into the enclosure. In general, these combats resembled those of *Lampropeltis getulus holbrooki* STEJNEGER, 1902 (CARPENTER 1977b), and the contestants did not bite each other. When the males fought for food (n = 33 times), the larger one almost always ended up eating the prey (81.8% of the cases, $\chi^2 = 6.68$, $df = 1$, $P < 0.05$), thus suggesting that body size is important for determining dominance in the combats between male *C. gemonensis*. Sexual combats of male *C. gemonensis* were already reported by STEMMLER-MORATH (1935), DAVIS (1936) and SHAW (1951). However, the behaviors of courtship and copulation have not been described in detail until now, and further research could be of value.

The Western Whip Snake - *Coluber viridiflavus* LACÉPÈDE, 1789, is the most common Italian snake but, despite this, its sexual behavior is still largely unknown. In the populations of Mediterranean Central Italy (Tolfa Mountains) the above-ground activity usually starts in March-April, the males emerging earlier than the females (FILIPPI 1995; CAPULA & al. (1997). In early spring several individuals were frequently found in close proximity to one another, and combats between males for access to females were observed on many occasions, usually during April when the mating season intensity peaks (CAPULA & al. (1997). In a single case (12 April 1995; 10.10 a. m. in European Standard Time), five males were involved in a fight in the presence of a female. The combats appeared ritualized, and the males did not bite at one another. However, these snakes are extremely quick and ready to disappear into bushes; so we never had the opportunity to observe any combat for more than a few seconds. Thus, we cannot be sure that biting is not a behavioral component of these male-male fights. GUIBE & SAINT GIRONS (1955) already reported on the occurrence of male-male fights in French populations of this taxon, but did not mention biting as a component of these interactions. Our field observations show that during courtship there is intensive toungue flicking between partners, with male-head-noddings and body contact relatively similar to those described for *Vipera berus* (ANDRÉN 1986). Copulating pairs were occasionally seen while basking in well-exposed spots, usually on dry substratum. A recent study carried out on free-ranging *C. viridiflavus* demonstrated that (i) adult females are usually able to bear every year, and (ii) also those unready for reproduction are attractive to males and participate in the population's sexual activity (CAPULA & al. 1995). This finding may have important consequences for the mating system of this species (see below).

The sexual behavior of the Horseshoe Whip Snake, - *Coluber hippocrepis* LINNAEUS, 1758, is completely unknown, and, thus, we cannot provide any information.

Coronella: This genus consists of two small sized (< 80 cm long) species. Both species are characterized by minor SSD (CAPULA & al. 1995b) and obvious sexual chromatic dimorphism (SHINE 1993). The reproductive mode of the Smooth Snake, *Coronella austriaca* LAURENTI, 1768, is live-bearing, while that of the Southern Smooth Snake, *C. girondica* (DAUDIN, 1803), is oviparity. In both species the males clench their teeth on the body of the female during copulation, that may last 6-7 hours (NAULLEAU 1984).

The males of *C. austriaca* vigorously and cruelly combat for access to females in

early spring. These combats were observed during early April in a Mediterranean area of central Italy (Oriolo Romano, Tolfa Mountains, about 450 m a.s.l.), and during mid to the end of May in an alpine locality (Sella Nevea, Carnic Alps, about 1100 m a.s.l.) where male Smooth Snakes emerge from winter inactivity later in April, soon after the snow cover melts (LUISELLI & al. 1996). In the eastern Alps the male-male combats were occasionally observed under stones, in the presence or absence of the females. Similar behavior was observed in Swedish Smooth Snakes (C. ANDRÉN, pers. comm.). Our experiments (still in progress) indicate that in these combats the bigger males win more often and drive the smaller ones away from the receptive females.

Also in *C. girondica* combats between males were observed from the end of April to mid-May in a Mediterranean locality of central Italy (Tolfa Mountains, about 250 m a.s.l.), at the edge of spiny bushes or under stones. In these combats the males bite their rivals vigorously but also use their tails for "lashing" the body of the enemy. The males sloughed before the beginning of the mating season, thus taking a bright pink-orange coloration in the flanks. We are actually experimenting under semi-natural conditions to see whether bright coloration has a communication value, and whether the individuals with more saturate coloration have higher mating success than the less coloured ones (as in some lizards, see OLSSON 1994a, 1994b; CAPULA & al. 1997). The concurrent presence of male-male combats and bright dorsal coloration suggests some convergence in traits of reproductive behavior between *C. girondica* and *V. berus* (see ANDRÉN 1986; LUISELLI 1995), despite these two taxa are neither phylogenetically related nor ecologically similar.

Elaphe: Four species of this genus are found in Italy; however, one of them - the Ladder Snake, *E. scalaris* (SCHINZ, 1822) - is known to occur in one locality only (DORIA & SALVIDIO 1994). All the species are oviparous, with no evident colour dimorphism between sexes. In most populations of the Aesculapian Snake - *Elaphe longissima* (LAURENTI, 1768), males are larger than females (NAULLEAU 1992), but the reverse situation is found in the other three species (POZIO 1976; FILIPPI 1995). All species of this genus are characterized by similar mating behavior (see GILLINGHAM 1979; BUTLER 1991). The male courts the female by continuously touching 'her' with 'his' chin and tongue, and biting 'her' in the nape. The female responds to this stimulation with uncoiling and stretching out completely, both animals showing rapid epidermic caudocephalic waves in this phase (see also BLASQUEZ 1994). Finally, the male inserts one hemipenis in the female cloaca. During this phase the epidermic waves become slower. The end of the mating is indicated by (1) the male releasing the female from the coital bite and (2) separation of the animals.

Fights between male *E. longissima* were frequently observed in April and May in several Mediterranean localities of central Italy (Tolfa Mountains, about 200-450 m a.s.l.). These fights occurred not only on the ground but also on trees and walls at more than 3 m above the ground. The combats were highly ritualized, without biting. As already observed by SHAW (1951), we noted that a high vertical stance of the head, neck and anterior trunk was a frequent posture in combats of male Aesculapian Snakes. Also in this species, however, it has been rather difficult to observe combats in nature for more than a few seconds, and thus we cannot be sure that biting is not a behavioral component of these male-male fights. Courtship and copulation of our captive animals was characterized by the typical coital biting of the male to the head or the anterior part of the body of the female; this behavior was already observed by LOTZE (1975). As already reported for *C. viridiflavus*, in *E. longissima* nearly all adult females are inseminated during the reproductive season, although some of them may not be ready to produce eggs (CAPULA & al. 1995a). The same has been observed by NAULLEAU (1992) in populations from western France.

Sexual combats are components of the reproductive biology also of the Four-Lined Snake - *E. quatuorlineata* (LACÉPÈDE, 1789), and of the Leopard Snake - *E. situla* (LINNAEUS, 1758) (see POZIO 1976, 1983). Some male-male combats of Four-Lined Snakes were observed in nature be-

tween mid-May and the beginning of June in a Mediterranean locality of central Italy (Rota, Tolfa Mountains, about 200 m a.s.l.). The males were seen biting their rivals vigorously in these combats. However, due to the very secretive habits of this species, nothing is known on the mating behavior of *E. quatuorlineata*. Copulations were observed in Mediterranean central Italy from late May to late June, usually in the afternoon (15.30 - 19.30, see FILIPPI 1995). The behavior displayed by copulating animals is similar to the one described above for the whole genus *Elaphe*. Additional information on this issue is given by POZIO (1976).

The sexual behavior of Italian *E. scalaris* is completely undescribed. However, detailed information has been reported on French and Spanish individuals. The copulatory behavior is nearly identical to that described above for the whole genus (BLASQUEZ 1994). The mating season lasts from April to the beginning of June in southern France (and thus, most probably in Italy as well, CHEYLAN & GUILLAUME 1993), and from 9 to 22 June in the SW Iberian Peninsula (BLASQUEZ 1994).

Our observations on *E. situla* come from three captive specimens only (two males and a female) maintained in an outdoor terrarium of 180 x 60 cm. In this enclosure the bigger male (77 cm long) fought repeatedly with the smaller one (68.5 cm long) during spring (March and April), excluding it from copulation with the female available. The combats were similar to those of *E. longissima* in some postures (SHAW 1951), but bites and prolonged pursuits were usual components of these fights. Some fights were very violent; the smaller animal in our cage finally died after about two months of continued aggressive actions through the stronger male. It is interesting to note that aggressive behavior did not only occur for access to the female, but also in competing for food.

Macroprotodon cucullatus (GEOFFROY, 1827): The sexual behavior of this very elusive species is still completely unknown. The information provided here comes from two adult males of Lampedusa Island that were held during spring 1996 in a cage of 100 x 60 cm. The males in our cage fought several times in spring (mid-April), despite no female being available. These combats lasted for 1-3 minutes only and were characterized by frequent biting.

Malpolon monspessulanus (HERMANN, 1804): This large sized (up to 2.5 m long, see BRUNO & MAUGERI 1990) oviparous psammophine snake, shows remarkable male-larger SSD and sex differences in colour, the males being uniform and the females being black spotted in the dorsal parts (DE HAAN 1994).

M. monspessulanus is probably one of the European colubrids with a more complex sexual and social behavior. The males combat for access to females during the mating season (mid-May to early June, see CHEYLAN & al. 1981), and remain vigilant over the female site for a prolonged time (DE HAAN 1984), showing a kind of "vigilance" behavior similar to that observed in *V. berus* (LUISELLI 1993a, 1993b, 1995; MADSEN & al. 1993) and *V. aspis* (SAINT GIRONS 1996). In *M. monspessulanus* the copulation can be voluntarily interrupted and quickly recommenced due to the peculiar structure of the male hemipenis (DE HAAN 1984). *M. monspessulanus* is also known for a kind of "rubbing" head behavior (DE HAAN 1982) which may serve for habitat and congener marking with chemical substances (DE HAAN 1993).

Telescopus fallax (FLEISCHMANN, 1831): This is one of the very rare species of Italy (LAPINI 1983), and its sexual behaviors are nearly unknown. It is not clear whether the males combat for access to females, and data on reproductive seasonality is very scarce and anecdotal (BRUNO & MAUGERI 1990). Coloration features are similar in the sexes (BRUNO & MAUGERI 1990), despite ZINNER (1985) reported on remarkable sex differences in colour in its congener *T. dhara* (FORSKÅL, 1776). The females are generally larger than males (BRUNO & MAUGERI 1990).

Alternative reproductive strategies and the potential for long-term sperm storage

The climatic types of the Italian Peninsula are rather diverse depending on the various regions and include the typical Mediterranean climate (in coastal, central

and southern Italy), the subcontinental Apennine climate (in the Apennines and in the Sardinian and Sicilian mountains), the subcontinental temperate Adriatic climate (in the Adriatic coast), the continental cool-temperate climate (in the Po river plain), and the continental cold Alpine climate (in the Alpine regions) (ACCORDI & LUPIA PALMIERI 1979). Despite this relative variety of mesothermic climates, all the Italian snake species show a similar reproductive seasonality, primarily determined by the length of the hibernation phase and by the reproductive mode. The reproductive seasonality of the Italian colubrids is well explained by that of *N. natrix* and *C. austriaca* in the eastern Alps (see LUISELLI & al. 1996, 1997). The former species can be used as a model for describing the reproductive seasonality of the oviparous snakes, the latter for the live-bearing snakes. *N. natrix* emerges from hibernation in late April (males earlier than females), copulation takes place in May, oviposition in the second part of July, and eggs hatch at the end of August. *C. austriaca* also emerges from hibernation in late April (males earlier than females) and has its mating season in May, but gives birth to young in late August or at the beginning of September. Spring mating (more or less immediately after the end of hibernation, depending also on the proximate climatic conditions), early summer oviposition and late summer hatching are, with minor local and species-specific differences, widespread patterns in Italian colubrids (see AGRIMI & LUISELLI 1994 for *C. girondica*, and CAPULA & al. 1995a for *C. viridiflavus* and *E. longissima*). The possibility of finding alternative reproductive strategies in Italian colubrids is thus very limited.

Spring births in cold (high-altitude) climates

From a locality of the extreme southern tip of Sweden, MADSEN (1989) reported on the very rare event of a female *V. berus* giving birth in spring (11th April 1988), despite young are usually born from August to early September in this species (NILSON 1981; CAPULA & al. 1992). MADSEN suggested that (i) this event was most likely caused by the cold summer in 1987, and (ii) the female which gave birth in spring had to enter hibernation while still gravid and the embryos were able to survive the hibernation period. He finally hypothesized that spring birth could be an alternative reproductive strategy in areas with shorter activity seasons for snakes at northern latitudes and / or high altitudes.

This alternative reproductive strategy was never observed in Alpine Adder populations from the higher elevations (2200-2500 m a.s.l., see CAPULA & LUISELLI 1992), and seems not to occur in the Italian colubrids, including both live-bearing and oviparous taxa. In this regard we have detailed data for two alpine populations of colubrids, and also some observations for populations inhabiting the Apennine massif. In the Alpine cool climate populations of *C. austriaca* and *N. natrix* all gravid females gave birth in late summer, without remarkable variations among individual females or among research years (CAPULA & al. 1995b, and unpublished observations; LUISELLI & al. 1996, 1997). Twenty-eight *C. austriaca* females studied in the eastern Italian Alps (Tarvisio Forest, province of Udine) for a period of five years (obtaining an average of 1.07 ± 0.60 litters each, with a range of 0 to 3) gave birth in late summer and did not show any significant annual variation in the dates of parturition (examining year- to-year variation by one-factor ANOVA with year as the factor: $F_{4,22}$=0.25, P=0.9), and the same was true for 20 *N. natrix* females of the same geographic area which oviposited always between 17 and 30 July without any year-to year difference (one-factor ANOVA with year as the factor: $F_{3, 10}$ = 1.48, P = 0.28). Moreover, 100% of the gravid females of *N. natrix* (n=11), *C. viridiflavus* (n=3) and *C. austriaca* (n=8) inhabiting a mountain area of the central Apennines (Velino Massif, about 1500 m a.s.l.) oviposited in late July (oviparous species) or gave birth to young at the beginning of September (live-bearing species), showing no remarkable difference with conspecifics from other geographic areas. Thus, our current data does not support MADSEN's (1989) hypothesis, although more data on high mountain populations of snakes is required before firm statements can be made.

Autumnal mating and long-term sperm storage

In several reptile species there may be long preservation of spermatozoa in the genital organs (usually in the vaginal segment of the oviduct) of females (SAINT GIRONS 1973). Theory suggests that sperm storage may evolve to secure reproduction in populations or species having weakly pronounced mating seasons (e. g., in tropical species with irregular and "unsynchronized" mating periods) and low densities (PORTER 1972). In European snake species long-term sperm storage is rare and restricted to populations showing not only the usual spring mating season but also a less intense autumnal mating season (e.g., some populations of *V. aspis*, *V. seoanei* and *V. latastei*; see SAINT GIRONS 1976). Thus, long-term sperm storage is not observed in *V. berus* and other species exclusively mating during springtime (ANDRÉN & NILSON 1987; LUISELLI 1993b, 1995; HOGGREN & TEGELSTROM 1996).

Literature data on the occurrence of long-term sperm storage in European snakes is still very scarce. To our knowledge, solely PARELLADA (1995) reported on a snake population (*V. latastei*) in which copulation was not observed in spring but only during autumn, thus indicating obligatory use of sperm storage as a reproductive strategy. However, this author's observations were done in an outdoor enclosure with relatively little evidence of similar phenomena occurring in nature. In all other cases reported, sperm storage appears to be merely an anomalous event linked to autumnal mating (SAINT GIRONS 1973). This was the case, for instance, in some individuals of *C. austriaca* (DUGUY 1961), *N. maura* (DUGUY & SAINT GIRONS 1966), and *N. natrix* (D'ABADIE 1928; NAULLEAU 1984). These two latter species are also known for some cases of exceptionally prolonged sperm survival in the female uterus (six years according to QUILLON & LAMOUILLE 1978).

Careful field studies excluded the occurrence of sperm storage in Alpine populations of *N. natrix* and *C. austriaca* from the Tarvisio Forest (about 1100 m a.s.l.) (LUISELLI & al. 1996, 1997). In this region an autumnal mating season is unlikely to occur due to the low ambient temperatures which constrain the snakes to retire into hibernation before the end of October (LUISELLI & al. 1996, 1997). On the other hand, an autumnal mating season is likely to occur in the Mediterranean regions where the mild climate permits prolonged autumnal activity of snake populations (until end of November or early December). However, despite careful research over several years (1985-1995), no autumnal copulation was seen in most of the colubrids of Mediterranean central Italy, including *N. natrix*, *N. tessellata*, *E. longissima*, *E. quatuorlineata*, *C. girondica*, and *C. viridiflavus* (AGRIMI & LUISELLI 1994; CAPULA & al. 1995a, 1995b; FILIPPI 1995; CAPIZZI & al. 1996). On the other hand, the occurrence of autumnal copulations was occasionally observed in *C. austriaca*: a mating pair was seen in Oriolo Romano (Tolfa Mountains, province of Viterbo, about 450 m a.s.l) on October 17, 1989, and another mating pair in the same locality on October 3, 1995. In these two cases the females were not collected, and it was thus impossible to establish whether autumnal copulations effectively resulted in their fecundation. A true case of long-term sperm storage was observed in *N. maura*: one out of five adult females collected during late October 1992 in a locality in central Sardinia (Giara di Gesturi, about 270 km southwest of Nuoro, 550 m a.s.l) oviposited on 3rd July 1993, despite no male has been housed in the terrarium. This female was 58.3 cm long, its clutch size was 7 eggs, and the mean egg size was 27.8 x 15.9 mm, which is much smaller than that of the eggs deposited by other *N. maura* which mated in spring ($\bar{x}$ = 29.6 x 16.8 mm, n = 135 eggs). Moreover, only one offspring hatched; it was born on August 7, 1993 (35 days after oviposition), measured 17.2 cm in total length and was in excellent health condition.

Recent field-work demonstrated that in a locality of Mediterranean central Italy (Tolfa Mountains, province of Rome) most of the female *C. viridiflavus* and *E. longissima* are inseminated during the intense spring mating season, although some of them are unready to produce eggs (CAPULA & al. 1995b). This finding, which is

probably valid for many other populations of European snakes (ANDRÉN & NILSON 1987; NAULLEAU 1992; LUISELLI 1993B; SAINT GIRONS 1996), is particularly relevant because it introduces a potential for long-term sperm storage in these animals. One could hypothesize that these inseminated females, unable to ovulate and produce eggs within-season, could preserve sperm in their genital organs. Ova could then be fertilized in the following year(s), when the female's body fat reserves necessary for reproduction will have finally restored. When we submitted the original CAPULA & al. (1995a) paper for publication (October 1994), we did not have enough data to draw firm conclusions on this issue, and thus preferred to avoid any discussion. But now we have much more data at hand. To test females for the occurrence of sperm storage, we housed several inseminated specimens from our previous study in terraria for a period of at least 365 days without males (see LUISELLI 1993b for an identical experimental procedure with *V. berus*). None of these females (8 *E. longissima* and 7 *C. viridiflavus*) produced eggs the year following insemination, despite their body condition being fit for reproduction (BCI > 0.55, see NAULLEAU 1992) due to substantial feeding on laboratory mice. Thus, we are led to conclude that these within-season inseminated non-reproductive females do not keep sperm in their genital organs.

DISCUSSION

Sexual fights among males were seen in 13 snake taxa (68.4% of the Italian snake fauna) and 21 populations. This proportion should probably be retouched because we had no available information on three very rare species. The sole taxa that seem to lack sexual fights are those of the genus *Natrix*, which are also the sole semi-aquatic snake species of Italy (BRUNO 1984; LUISELLI & RUGIERO 1991; FILIPPI 1995). However, at least in one of these species (*N. natrix*) physical interactions between males simultaneously courting single females may lead to a kind of "pseudocombat" where male body size is important for increasing the individual reproductive success (MADSEN & SHINE 1993; LUISELLI 1996). Sexual combats were found in species where males are bigger than females (n = 5), in species with minor SSD (n = 4), and in species with significantly reversed SSD (n = 4). Excluding the three species for which data are not available, 100% of the taxa with minor SSD or with male-larger dimorphism showed sexual combats, but only 57.1% of those with reversed SSD. This consideration empirically supports the conclusion that male-larger dimorphism and occurrence of sexual combats are correlated in snakes (SHINE 1978, 1993, 1994).

Ritualized combats without biting ("type 1") occurs in 8 species (four viperids and four colubrids), while "type 2" is typical to two species (*C. austriaca, M. cucullatus*), "type 3" to one species (*C. girondica*) and "type 4" to two *Elaphe*. Interestingly, "type 2" is present in two taxa that, although phylogenetically unrelated, have semi-fossorial habits and convergent morphological traits (WADE 1988; BUSACK & MCCOY 1990; PLEGUEZUELOS & al. 1994). Biting is present only in non-venomous species (genera *Coronella, Elaphe* and *Macroprotodon*); this also agrees with SHINE's (1994) conclusions. The combats we assisted at were all harmless to the rivals, except those of *E. situla* which were occasionally so cruel that a captive male in our cages killed a smaller contestant. This should be considered as one of a few cases of male-male combat departing considerably from the typical highly ritualized dance, thus, resulting in combat fatality [see also PERRY-RICHARDSON 1991, for *Chondropython viridis* (SCHLEGEL, 1872)]. Interestingly, whilst sexual combats were omnipresent in the live-bearing taxa (n = 5 species, 100% of the cases), the same agonistic behavior was present only in 72.7% of the oviparous ones (n = 11 species). Moreover, sexual combats were exhibited both by alpine and Mediterranean snake populations (see table 1).

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REFERENCES

ACCORDI, B. & LUPIA PALMIERI, E. (1979): Il globo terrestre e la sua evoluzione.- Bologna (Zanichelli), 393 pp.

AGRIMI, U. & LUISELLI, L. (1994): Ecology of the snake *Coronella girondica* (Reptilia, Colubridae) in central Italy.- Vie et Milieu; 44: 203-210.

ANDRÉN, C. (1986): Courtship, mating and agonistic behavior in a free-living population of adders, *Vipera berus* (L.).- Amphibia-Reptilia; 7: 353-383.

ANDRÉN, C. & NILSON, G. (1987): The copulatory plug of the adder, *Vipera berus*: does it keep sperm in or out?- Oikos; 49: 230-232.

ANDRÉN, C. & NILSON, G. (1992): *Coronella austriaca*.- Norges Dyr. Vol. 3, Krypdyr, Amfibier, Fiskes. Oslo (J. W. Cappelens forlag A/S) [Norwegian].

BLASQUEZ, M. C. (1994): Notes on the reproduction of *Elaphe scalaris* (SCHINZ, 1822) in southern Spain.- Herpetol. J.; 4: 109-111.

BRUNO, S. & MAUGERI, S. (1990): Serpenti d' Italia e d'Europa.- Milano (Editoriale Giorgio Mondadori).

BUTLER, R. (1991): Notes on the keeping and breeding of the ladder snake, *Elaphe scalaris*.- Herptile; 16: 28-34.

CAPIZZI, D. & CAPULA, M. & EVANGELISTI, F. & FILIPPI, E. & LUISELLI, L. & TRUJILLO JESUS, V. (1996): Breeding frequency, clutch size, reproductive status and correlated behaviors in sympatric females *Elaphe quatuorlineata* and *Elaphe longissima* (Reptilia: Colubridae).- Revue d'Ecologie (Terre et Vie); 51: 297-311.

CAPULA, M. & FILIPPI, E. & LUISELLI, L. (1995a): Annual mating in female colubrid snakes with irregular reproductive frequency.- Herpetozoa; 8: 11-15.

CAPULA, M. & FILIPPI, E. & LUISELLI, L. & TRUJILLO JESUS, V. (1997): The ecology of the Western Whip Snake, *Coluber viridiflavus* in Mediterranean Central Italy.- Herpetozoa, Vienna; 10 (1/2): 65 - 79.

CAPULA, M. & LUISELLI, L. (1992): Ecology and phenology of *Vipera berus* populations (Reptilia, Viperidae) from eastern Italian Alps. In: KORSOS, Z. & KISS, I. (eds.): Proc. 6th Ordinary General Meeting of the Societas Europaea Herpetologica, Budapest; pp. 95-99.

CAPULA, M. & LUISELLI, L. (1994): Can female adders multiply?- Nature, London; 369: 528.

CAPULA, M. & LUISELLI, L. & ANIBALDI, C. (1992): Complementary study on the reproductive biology in female adder, *Vipera berus* (L.) from eastern Italian Alps.- Vie et Milieu; 42: 327-336.

CAPULA, M. & LUISELLI, L. & CAPANNA, E. (1997, in press): The blue-spotted morph of the slow worm, *Anguis fragilis*: Colour polymorphism and predation risks.- Italian J. Zool.; 44.

CAPULA, M. & LUISELLI, L. & RUGIERO, L. (1995b): Ecological correlates of reproductive mode in reproductively bimodal snakes of the genus *Coronella*.- Vie et Milieu; 45: 167-175.

CARPENTER, C. C. (1977a): Communication and displays of snakes.- American Zoologist; 17: 217-223.

CARPENTER, C. C. (1977b): A combat ritual between two male speckled kingsnakes (*Lampropeltis getulus holbrooki*: Colubridae, Serpentes) with indications of dominance.- Southwestern Naturalist; 22: 517-524.

CARPENTER, C. C. (1986): An inventory of ritual combats in snakes.- Smithsonian Herpetol. Inf. Service; 69: 1-18.

CHEYLAN, M. & BONS, J. & SAINT GIRONS, H. (1981): Existence d'un cycle spermatogénétique vernal et prénuptial chez un Serpent méditerranéen, la Couleuvre de Montpellier, *Malpolon monspessulanus* (HERMANN) (Reptilia, Colubridae).- Comptes Réndus Acad. Sci., Paris; 292 (23): 1207-1209.

CHEYLAN, M. & GUILLAUME, C.-P. (1993): *Elaphe scalaris* (SCHINZ, 1822) - Treppennatter; pp. 397-430. In: BÖHME, W. (ed.): Handbuch der Reptilien und Amphibien Europas. vol. 3/I, Schlangen (Serpentes) I; Wiesbaden (Aula).

DAVIS, D. D. (1936): Courtship and mating behavior in snakes.- Field Mus. Nat. Hist., Chicago; (Zool. Ser.): 20: 257-290.

D'ABADIE, R. (1928): Accouplement automnal chez la Couleuvre à collier et la Vipère aspic.- Rev. Hist. Nat. Appl.; 9: 336-337.

DE HAAN, C. (1982): Description du comportement de "frottement" et notes sur la reproduction et la fonction maxillaire de la Couleuvre de Montpellier, *Malpolon monspessulanus*. Remarques comparatives avec *Malpolon moilensis* et *Psammophis* ssp.- Bull. Soc. Herpétol. France; 23: 35-49.

DE HAAN, C. (1984): Dimorphisme et comportement sexuel chez *Malpolon monspessulanus*. Considérations sur la dénomination subspécifique *insignitus*.- Bull. Soc. Herpétol. France; 30: 19-26.

DE HAAN, C. (1993): Social behavior and sexual dimorphism in the Montpellier snake *Malpolon monspessulanus* (Colubridae; Psammophiini).- Abstracts 7th Ordinary General Meeting Societas Europaea Herpetologica, Barcelona, p. 76.

DORIA, G. & SALVIDIO, S. (1994): Atlante degli anfibi e rettili della Liguria. Catalogo dei beni culturali della regione Liguria, Genova.

DUGUY, R. (1961): Le cycle annuel d'activité chez *Coronella austriaca*.- Revue d'Ecologie (Terre et Vie); 1961: 401-435.

DUGUY, R. & SAINT GIRONS, H. (1966): Cycle annuel d'activité et reproduction de la Couleuvre vipérine, *Natrix maura* (L.).- Revue d'Ecologie (Terre et Vie); 1966: 423-457.

FILIPPI, E. (1995): Aspetti dell'ecologia di due comunità di colubridi e viperidi (Reptilia: Serpentes) di un'area dell'Italia centrale (Monti della Tolfa, Lazio).- Unpublished Thesis, University of Rome "La Sapienza".

FILIPPI, E. & CAPULA, M. & LUISELLI, L. & AGRIMI, U. (1996): The prey spectrum of *Natrix natrix* (LINNAEUS, 1758) and *Natrix tessellata* (LAURENTI, 1768) in sympatric populations.- Herpetozoa; 8: 155-164.

FRETEY, J. (1987): Guide des Amphibiens et

Reptiles de France. Paris (Hatier).

GENT, A. H. (1988): Movement and dispersion of the smooth snake *Coronella austriaca* LAURENTI in relation to habitat.- Unpublished Ph.D. Thesis, University of Southampton, U.K.

GILLINGHAM, J. C. (1979): Reproductive behavior of the Rat snakes of the Eastern North America, genus *Elaphe*.- Copeia; 1979: 319-331.

GODDARD, P. (1981): Ecology of the smooth snake *Coronella austriaca* LAURENTI in Britain.- Unpublished Ph.D. Thesis, University of Southampton, U.K.

GUIBE, J. & SAINT GIRONS, H. (1955): Espace vital et territoire chez les reptiles.- La Nature, Paris; 3245: 358-362.

HOGGREN, M. & TEGELSTROM, H. (1996): Does long-term storage of spermatozoa occur in the adder (*Vipera berus*)?- J. Zool., London; 240: 501-510.

LAPINI, L. (1983). Anfibi e rettili (del Friuli-Venezia Giulia). Tricesimo (Carlo Lorenzini editore).

LOTZE, U. (1975): Zum Paarungsverhalten der Askulapnatter, *Elaphe longissima*.- Salamandra; 11: 67-76.

LUISELLI, L. (1993a): High philopatry can produce strong sexual competition in male adders, *Vipera berus*.- Amphibia-Reptilia; 14: 310-311.

LUISELLI, L. (1993b): Are sperm storage and within-season multiple mating important components of the adder reproductive biology?- Acta Oecologica; 14: 705-710.

LUISELLI, L. (1995): The mating strategy of the European adder, *Vipera berus*.- Acta Oecologica; 16: 375-388.

LUISELLI, L. (1996): Individual success in mating balls of the grass snake, *Natrix natrix*: Size is important.- J. Zool., London, 239: 731-740.

LUISELLI, L. & CAPULA, M. & SHINE, R. (1996): Reproductive output, costs of reproduction and ecology of the smooth snake, *Coronella austriaca*, in the eastern Italian Alps.- Oecologia; 106: 100-110.

LUISELLI, L. & CAPULA, M. & SHINE, R. (1997): Food habits, growth rates and reproductive biology of grass snakes, *Natrix natrix* (Colubridae) in the Italian Alps.- J. Zool., London; 241: 371-380.

MADSEN, T. (1983): Growth rates, maturation and sexual size dimorphism in a population of grass snakes, *Natrix natrix*, in southern Sweden.- Oikos; 40: 277-282.

MADSEN, T. (1984): Movements, home range size and habitat use of radio-tracked grass snakes (*Natrix natrix*) in southern Sweden.- Copeia; 1984: 707-713.

MADSEN, T. (1987): Cost of reproduction and female life-history tactics in a population of grass snakes, *Natrix natrix*, in southern Sweden.-Oikos; 49: 129-132.

MADSEN, T. (1989): Female adder (*Vipera berus*) in southern Sweden recorded giving birth in spring.- Amphibia-Reptilia; 10: 88-89.

MADSEN, T. & SHINE, R. (1993a): Male mating success and body size in European grass snakes.- Copeia; 1993: 561-564.

MADSEN, T. & SHINE, R. (1993b): Phenotypic plasticity in body sizes and sexual size dimorphism in European grass snakes.- Evolution; 47: 321-325.

MADSEN, T. & SHINE, R. & LOMAN, J. & HAKANSSON, T. (1993): Determinants of mating success in male adders, *Vipera berus*.- Animal Behavior; 45: 491-499.

NAULLEAU, G. (1984): Les serpents de France.- Revue Francaise d'Aquariologie et Herpetologie; 11: 1-56.

NAULLEAU, G. (1992): Reproduction de la couleuvre d'Esculape *Elaphe longissima* LAURENTI (Reptilia, Colubridae) dans le centre ouest de la France.- Bull. Soc.Herpétol. France; 62: 9-17.

NILSON, G. (1981): Ovarian cycle and reproductive dynamics in the female adder, *Vipera berus* (Reptilia, Viperidae).- Amphibia-Reptilia; 2: 63-82.

OLSSON, M. (1994a): Why are sand lizards (*Lacerta agilis*) not equally green?- Behavioral Ecology and Sociobiology; 35: 169-173.

OLSSON, M. (1994b): Nuptial coloration in the sand lizard, *Lacerta agilis*: An intra-sexually selected cue to fighting ability.- Animal Behavior; 48: 607-613.

PARELLADA, X. (1995): About the apparent inexistence of a spring mating in the Catalan population of *Vipera latastei* (Reptilia: Viperidae), and note about the reproductive success. pp. 250-254. In: LLORENTE, G. A. & MONTORI, A. & SANTOS X. & CARRETERO, M. A. (eds.): Scientia Herpetologica. Barcelona (Asociacíon Herpetológica Española).

PORTER, K. R. (1972): Herpetology. Philadelphia (Saunders).

POZIO, E. (1973): The biology of free-living and captive *Elaphe situla*.- Litteratura Serpentium; 3: 50-60.

POZIO, E. (1976): La biologia e il ciclo di vita di *Elaphe quatuorlineata* (LACÉPÈDE).- Bull. Soc. Zool. France; 101: 741-746.

QUILLON, J. & LAMOUILLE, M. (1978): A propos d'éclosions chez les Couleuvres *Natrix natrix* et *Natrix maura*.- Bull. Soc. Herpétol. France; 8: 18-28.

RUGIERO, L. & LUISELLI, L. (1996): Ecological notes on an isolated population of the snake *Elaphe quatuorlineata* (Colubridae).- Herpetol. J.; 6: 53-55.

SAINT GIRONS, H. (1973): Deplacements et survie des spermatozoides chez les reptiles. In "Transport, survie et pouvoir fécondant des spermatozoides chez les vertebrés, Paris (Colloques de l'Institut National de la Santé et de la Recherche Médicale); pp. 259-282.

SAINT GIRONS, H. (1976): Les différents types de cycle sexuel des males chez les Vipères européennes.- Comptes Réndus Acad. Sci., Paris; 282: 1017-1019.

SAINT GIRONS, H. (1996): Structure et évolution d'une petite population de *Vipera aspis* (L.) dans une région de bocage de l'ouest de la France.- Revue d'Ecologie (Terre et Vie); 51: 223-241.

SEIGEL, R. A. (1993): Summary: future research on snakes, or how to combat "lizard envy"?, pp. 395-402. In: SEIGEL, R. A. & COLLINS, J. T. (eds.): Snakes: ecology and Behavior. New York (McGraw-Hill Inc).

SHAW, C. E. (1951): Male combat in American colubrid snakes with remarks on the combat in other colubrid and elapid snakes.- Herpetologica; 7: 149-168.

SHINE, R. (1978): Sexual size dimorphism and male combats in snakes.- Oecologia; 33: 269-278.

SHINE, R. (1993): Sexual dimorphism in snakes, pp. 49-86. In: SEIGEL, R. A. & COLLINS, J. T. (eds): Snakes: ecology and behavior. New York (McGraw-Hill, Inc.).

SHINE, R. (1994): Sexual size dimorphism in snakes revisited.- Copeia; 1994: 326-346.

STEMMLER-MORATH, C. (1935): Beitrag zur Fortpflanzungsbiologie europaischer Colubridae.- Zool. Garten.; 8: 38-41.

SVENSSON, A. M. (1994): Radiopejling av Hasselsnoken (*Coronella austriaca* LAURENTI, 1768) (Colubridae).- Unpublished Thesis, University of Göteborg, Sweden.

ZIMMERMANN, P. & FACHBACH, G. (1996):

Verbreitung und Biologie der Würfelnatter, *Natrix tessellata tessellata* (LAURENTI, 1768) in Styria (Austria).- Herpetozoa; 8: 99-124.

ZINNER, H. (1985): On behavioral and sexual dimorphism of *Telescopus dhara* FORSCAL, 1776 (Reptilia: Serpentes, Colubridae).- J. Herpetol. Assoc. Africa; 31: 5-6.

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