

Annual mating in female colubrid snakes with irregular reproductive frequency (Squamata: Serpentes: Colubridae)

Jährliche Paarung bei weiblichen Colubriden mit unregelmäßigem
Fortpflanzungsrhythmus
(Squamata: Serpentes: Colubridae)

MASSIMO CAPULA & ERNESTO FILIPPI & LUCA LUISELLI

KURZFASSUNG

Weibliche Schlangen gemäßigter Klimate benötigen häufig mehr als eine Saison der Nahrungsaufnahme und Vitellogenese, um ein Gelege zu produzieren. In jedem Jahr der Fortpflanzung können sich Weibchen dabei mehrmals und mit mehreren Männchen paaren. Es ist jedoch weitgehend unbekannt, ob adulte, in der o. a. Weise nicht fortpflanzungsbereite Weibchen dennoch für Männchen attraktiv sind und an den sexuellen Aktivitäten der Population teilnehmen.

Zwei Colubriden des mediterranen Mittelitalien, *Coluber viridiflavus* LACÉPEDE, 1789 und *Elaphe longissima* (LAURENTI, 1768), wurden in dieser Hinsicht untersucht. Beide Arten haben eine ausgeprägte Frühjahrs-Paarungszeit (von Mitte März bis Ende Mai). Spermien fanden sich im Kloakenschleim von 95 % aller fortpflanzungsbereiten und nicht fortpflanzungsbereiten (d. h. mit Korpulenzfaktor $< 0,55$) Weibchen, die während oder unmittelbar nach der Paarungszeit gefangen wurden. Wir schließen daraus, daß der physiologische Zustand nicht fortpflanzungsbereiter Weibchen keinen signifikanten Einfluß auf ihr Auffinden durch paarungswillige Männchen ausübt.

ABSTRACT

Female snakes from temperate regions frequently require more than one season of feeding and vitellogenesis to produce clutches. In each reproductive year female snakes can mate several times and with several males. However, it is largely unknown whether adult females which are unable to produce clutches are attractive to males and participate in the sexual activity of the population.

Two colubrids from Mediterranean Central Italy, *Coluber viridiflavus* LACÉPEDE, 1789 and *Elaphe longissima* (LAURENTI, 1768), were studied in this respect. In both species there is a pronounced vernal mating season (from middle of March to the end of May). Spermatozoa were present in the cloacal mucus of about 95 % of all reproductive and non-reproductive (i. e. with Body Condition Index [BCI] < 0.55) female snakes captured during or immediately after mating season. Based on this evidence, we conclude that the physiological status of adult non-reproductive females does not significantly affect their localization by males ready to mate.

KEYWORDS

Elaphe longissima, *Coluber viridiflavus*, reproductive biology, mating, female attraction; Central Italy

INTRODUCTION

In several live-bearing and oviparous snake species from temperate regions the females' 'per-offspring-costs' of vitellogenesis and folliculogenesis are much higher than those spent in spermatogenesis by the males (DUVALL & al. 1992). As a primary consequence, males typically exhibit annual spermatogenic cycles also in cold climates (ALDRIDGE 1979; SAINT GIRONS 1982, 1993; DUVALL & al. 1992), while females often require more than one season of feeding and vitellogenesis to produce clutches (e. g. biennial, tri-

ennial cycles - KLAUBER 1936; SAINT GIRONS 1957; TINKLE 1962; SAINT GIRONS & KRAMER 1963; LUISELLI & al. i. press).

Moreover, the female frequency of reproduction is often irregular since time for reconstruction of the fat reserves necessary for clutch production can vary significantly among individuals being influenced by factors such as climate, prey availability, body size, and dorsal coloration (FITCH 1970; ALDRIDGE & SEM-LITSCH 1992; CAPULA & LUISELLI

1994a). Thus, at the beginning of the mating season, snake populations can include both adult females ready for giving birth and adult females with insufficient body reserves and unready for doing so (BONNET & NAULLEAU 1994).

Females ready for clutch production actively participate in the population's sexual activity and can mate frequently and with several males within season (STILLE & al. 1987; MADSEN & al. 1992; CAPULA & LUISELLI 1994b). However, because of insufficient field data, it is largely unknown whether adult females which are unable to produce clutches are attractive to males and participate in the population's sexual activity.

NAULLEAU (1992) observed that all the female *Elaphe longissima* (LAURENTI, 1768) studied in Central France copulated in the mating season, though some of them (with Body Condition Index [BCI] < 0.55) did not produce litter after insemination. Similar observations were made in female Asp Vipers, *Vipera aspis* (SAINT GIRONS 1957), and Adders, *V. berus* (LINNAEUS, 1758) from the eastern Alps.

These snakes copulate annually but usually reproduce in alternate years (LUISELLI 1993; CAPULA & LUISELLI 1994a). Moreover, in southern Sweden, sperm was always found in female Adders from the beginning of the mating season until middle of June, once again demonstrating the occurrence of annual mating in females of this viper (NILSON 1981a, 1981b; ANDRÉN & NILSON 1987). Thus, annual mating appears to be normal in female snakes whereas reproduction may not be annual.

In our paper we present new data on this subject. We examined female snakes that were captured during or immediately after mating season (1) regarding presence or absence of spermatozoa in their cloacal mucus, and checked (2) whether the inseminated females produced clutches or not.

For this purpose we selected the Western Whip Snake (*Coluber viridiflavus* LACÉPEDE, 1789) and the Aesculapian Snake (*E. longissima*), both widespread in Mediterranean Central Italy, as model species.

MATERIALS AND METHODS

The study was conducted in Mediterranean Central Italy (Tolfa Mountains, 300-450 m a.s.l., about 60 km North of Rome, Latium), where several long-term studies on snake ecology have been carried out so far (LUISELLI & AGRIMI 1991). The habitats of the snakes are 'bushy pastures' with discontinuous populations of *Spartium*, *Paliurus*, *Cytisus*, *Rubus*, and localized stands of *Pirus pyrastrer* at the edge of *Fagus* and *Quercus* woodlands. The study began in spring 1993; most data were collected in spring 1994.

Adult female *E. longissima* and *C. viridiflavus* (adults were easily recognized because of the great ontogenetical change of dorsal coloration - BRUNO 1984) were captured by hand, measured (to ± 0.5 cm), weighed (to ± 0.1 g), and scale-clipped. Cloacal smears were taken by slight massage of the posterior part of the snakes' bodies. The mucus was examined in the

laboratory for the presence of spermatozoa (FUKADA 1959; NAULLEAU 1986, 1992). The reproductive status and the approximate timing of ovulation of the inseminated female snakes were determined by palpation of the abdomen. In Whip Snakes this was chiefly done when they were later recaptured in the field (normally at about middle of June), whereas most *E. longissima* were housed in captivity until ova were palpable. This procedure was necessary as Aesculapian Snakes may be very elusive and, thus, difficult to recapture in late spring and early summer.

A total of 102 female *C. viridiflavus* and 38 female *E. longissima* was examined for the presence of spermatozoa in the cloacal mucus. The reproductive status of 48 out of 97 inseminated female *C. viridiflavus* and 31 out of 36 inseminated female *E. longissima* was determined from the pooled specimens both housed in ter-

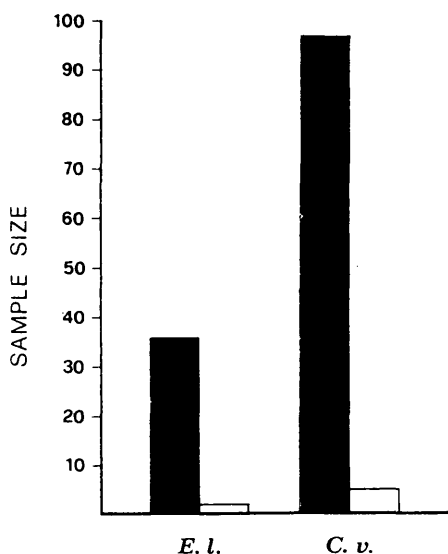


Fig. 1: Number of female *Coluber viridiflavus* and *Elaphe longissima* with (black columns) and without (white columns) spermatozoa in the cloacal mucus. The specimens were captured during and immediately after mating season in Central Italy (Tolfa Mountains, province of Rome, Latium).

Abb. 1: Anzahl weiblicher *Coluber viridiflavus* und *Elaphe longissima* mit (schwarze Säulen) und ohne (weiße Säulen) Spermien im Kloakal-schleim. Die Individuen wurden während oder kurz nach der Paarungszeit in Mittelitalien (Tolfa Berge, Provinz Rom, Latium) gefangen.

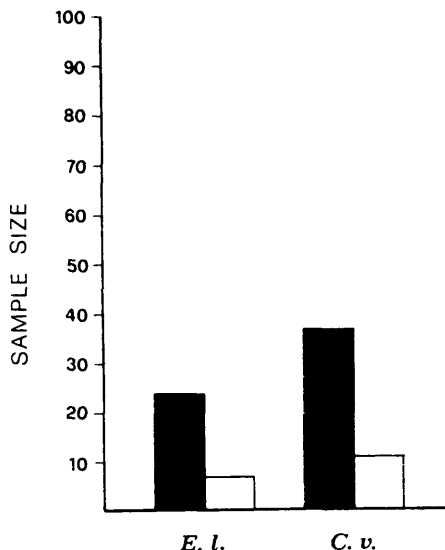


Fig. 2: Number of inseminated female *Coluber viridiflavus* and *Elaphe longissima* that produced (black columns) and did not produce (white columns) clutches in the current year. The sample is composed of recaptured or caged specimens out of those analyzed in table 1.

Abb. 2: Anzahl besamter weiblicher *Coluber viridiflavus* und *Elaphe longissima*, die im Untersuchungs-jahr Gelege (schwarze Säulen) und die keine Gelege (weiße Säulen) produzierten. Die Stichprobe setzt sich aus in Abbildung 1 untersuchten wiedergefangenen oder gehälterten Individuen zusammen.

raria and recaptured in the field.

We also describe the reproductive phenology of the taxa based on observation of mating individuals in captivity as well as on inferences from the amount of spermatozoa found in the female cloacal mucus (FUKADA 1959; NAULLEAU 1992).

When necessary, we determined a

snake's body condition by calculating its Body Condition Index (BCI, see LELOUP 1976): $BCI = BMR / BMT$. In this formula, BMR is the real body mass of the snake, while BMT is the theoretic body mass [$BMT = (\text{length of the snake} / \text{average offspring length})^3 \times (\text{average offspring mass})$].

RESULTS AND DISCUSSION

In *E. longissima* mating was observed from middle of April to the end of May, ovulation generally occurred in the

middle of June, and eggs were laid at the end of July. In *C. viridiflavus* mating occurred from middle of March to the end of

April (rarely to the middle of May), ovulation took place at the beginning of June, and eggs were laid from the end of June to the middle of July. The above reproductive phenologies are similar to those correspondingly reported for Whip Snakes and Aesculapian Snakes in Central France (NAULLEAU 1987, 1992).

Spermatozoa were detected in the female cloacal mucus of about 95 per cent of Whip Snakes and Aesculapian Snakes (fig. 1).

77 per cent of the inseminated female *C. viridiflavus* (37 out of 48) and 77.4 per cent of the inseminated female *E. longissima* (24 out of 31) produced eggs. Interspecific difference in these frequencies was not significant (*Chi*² test; *df* = 1; fig. 2). Considering that in snakes a single mating seems to be sufficient to fertilize ova (STILLE & al. 1986; MADSEN & al. 1992), we suggest that these females were unable to reproduce simply because of their insufficient fat body reserves at the time of copulation.

This suggestion is largely supported by the fact that the Body Condition Indexes [BCI] (immediately after the end of the mating season) of all inseminated but non-reproductive Aesculapian and Whip Snake females was $<< 0.55$, a threshold value that female *E. longissima* should exceed for reproduction to take place (NAULLEAU 1992; BONNET & NAULLEAU 1994). Further evidence in favour of the above suggestion comes from the field record of a copulating pair of *C. viridiflavus*

(male: 122 cm, 208 g; female: very emaciated, 114 cm, 109 g) at Oriolo Romano (Tolfa Mountains, 450 m a.s.l.) observed on April 14th, 1994. This female displayed poor body condition and in fact did not produce a clutch within season.

Nearly all adult female *C. viridiflavus* and *E. longissima* of the studied populations - whether ready or unready to give birth - copulated during their reproductive period. Based on this evidence and though our data are preliminary, we conclude that there is no reason to assume that non-breeding females were sexually non-receptive or at least unattractive to males in mating disposition.

Male snakes usually localize females by following their pheromone trails using the lipoprotein vitellin and other related volatile semio-chemicals for conspecific recognition (KUBIE & HALPERN 1975; GARSTKA & CREWS 1981; MASON & CREWS 1985; FORD 1986; GILLINGHAM 1987), or by visual cues (GILLINGHAM 1979). Considering this, it appears reasonable to hypothesize that neither olfactory nor non-olfactory localization of females by males is significantly affected by the non-receptivity adult females.

The biological meaning of the lack of unattractiveness of non-reproductive females to males is not clear, and further studies should be carried out, also for determining whether this phenomenon is widespread among snakes.

ACKNOWLEDGMENTS

The authors are gratefully indebted to U. AGRIMI (Istituto Superiore di Sanità, Rome) for help in the field and critical comments on an earlier draft. H. FUKADA (University of Kyoto, Japan), G. NAULLEAU (C. N. R. S., Chizé, France), H. SAINT GIRONS (University of Paris, France), and R. SHINE (University of Sydney, Australia) kindly provided papers cited in the text. The contents of this

paper were improved by useful discussions with G. NAULLEAU and J.-C. MONNEY (University of Neuchâtel, Switzerland). Financial support was provided by the Italian Ministero dell'Università e della Ricerca Scientifica e Tecnologica (M. U. R. S. T., 40%) and Consiglio Nazionale delle Ricerche (C. N. R., grant 91.00655.CT04), funded to E. CAPPANNA (University of Rome "La Sapienza").

REFERENCES

- ALDRIDGE, R. D. (1979): Seasonal spermatogenesis in sympatric *Crotalus viridis* and *Arizona elegans* in New Mexico.- *J. Herpetol.*; 13: 187-192.
- ALDRIDGE, R. D. & SEMLITSCH, R. D. (1992): Female reproductive biology of the South-eastern Crowned Snake (*Tanilla coronata*).- *Amphibia-Reptilia*; 13: 209-218.
- ANDREN, C. & NILSON, G. (1987): The copulatory plug of the Adder, *Vipera berus*: Does it keep sperm in or out? - *Oikos*; 49: 230-232.
- BONNET, X. & NAULLEAU, G. (1994): Utilisation d'un indice de condition corporelle (BCI) pour l'étude de la reproduction chez les serpents.- *C.*

- R. Acad. Sci. Paris: (Sciences de la vie) 317: 34-41.
- BRUNO, S. (1984): Guida ai serpenti d'Italia; Firenze (Giunti Martello). 191 pp.
- CAPULA, M. & LUISELLI, L. (1994a): Reproductive strategies in alpine Adders, *Vipera berus*. The black females bear more often.- Acta oecol.; 15: 207-214.
- CAPULA, M. & LUISELLI, L. (1994b): Can female adders multiply? - Nature; 369: 528.
- DUVALL, D. & ARNOLD, S. J. & SCHUETT, G. W. (1992): Pitviper mating systems: Ecological potential, sexual selection and microevolution. In: CAMPBELL, J. A. & BRODIE, E. D. (eds.): Biology of the Pitvipers. pp. 321-336. Tyler Texas (Selva).
- FITCH, H. S. (1970): Reproductive cycles of lizards and snakes.- Univ. Kansas Mus. Nat. Hist. Misc. Publ.; 52: 1-247.
- FORD, N. B. (1986): The role of pheromone trails in the sociobiology of snakes; In: DUVALL, D. & MÜLLER-SCHWARZE, D. & SILVERSTEIN, R. (eds.): Chemical signals in vertebrates. New York (Plenum Press).
- FUKADA, H. (1959): A method for detecting copulated female snakes.- Herpetologica; 15: 181-182.
- GARSTKA, W. R. & CREWS, D. (1981): Female sex pheromones in the skin and circulation of a Garter Snake.- Science; 214: 681-683.
- GILLINGHAM, J. C. (1979): Reproductive behavior of the Rat Snakes of eastern North America, genus *Elaphe*.- Copeia 1979: 319-331.
- GILLINGHAM, J. C. (1987): Social behavior; In: SEIGEL, R. A. & COLLINS, J. T. & NOVAK, S. S. (eds.): Snakes: Ecology and evolutionary biology, pp. 184-209. New York (MacMillan)
- KLAUBER, L. M. (1936): A statistical study of the Rattlesnakes. I. Introduction.- Occ. Papers San Diego Soc. Nat. Hist.; 1: 1-24.
- KUBIE, J. & HALPERN, M. (1975): Laboratory observations of trailing behavior in Garter Snakes.- J. Comp. Physiol. Psychol.; 89: 667-674.
- LELOUP, P. (1976): Méthode simple pour calculer approximativement et comparativement les matières de réserve des serpents vivants.- Acta Zool. Pathol., Antwerpen; 64: 91-93.
- LUISELLI, L. (1993): Are sperm storage and within-season multiple mating important components of the Adder reproductive biology? - Acta oecol.; 14: 705-710.
- LUISELLI, L. & AGRIMI, U. (1991): Composition and variation of the diet of *Vipera aspis francisciredi* in relation to age and reproductive stage.- Amphibia-Reptilia; 12: 137-144.
- LUISELLI, L. & CAPULA, M. & SHINE, R. (in press): Reproductive output, costs of reproduction and ecology of the Smooth Snake (*Coronella austriaca*) in the eastern Italian Alps.- Oecologia.
- MADSEN, T. & SHINE, R. & LOMAN, J. & HAKANSSON, T. (1992): Why do female Adders copulate so frequently? - Nature; 355: 440-441.
- MASON, R. T. & CREWS, D. (1985): Analysis of sex attractant pheromone in Garter Snakes.- American. Zoologist; 25: 76A (abstract).
- NAULLEAU, G. (1986): Effects of temperature on 'gestation' in *Vipera aspis* and *Vipera berus* (Reptilia, Serpentes); In: ROCEK, Z. (ed.): Studies in herpetology, pp. 489-494. Prague (Charles University).
- NAULLEAU, G. (1987): Les serpents de France.- Rev. Française Aquar. Herpetol.; 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. Herpetol. France; 62: 9-17.
- NILSON, G. (1981a): Endocrine and ecological interrelations in reproduction of the Adder, *Vipera berus* (L.); Ph. D. Thesis, Univ. Göteborg (unpublished).
- NILSON, G. (1981b): Ovarian cycle and reproductive dynamics in the female Adder, *Vipera berus* (Reptilia, Viperidae).- Amphibia-Reptilia; 2: 63-82.
- SAINT GIRONS, H. (1957): Le cycle sexuel de *Vipera aspis* dans l'ouest de la France.- Bull. Biol. France Belg.; 151: 284-360.
- SAINT GIRONS, H. (1982): Reproductive cycles of male snakes and their relationships with climate and female reproductive cycle.- Herpetologica; 38: 5-16.
- SAINT GIRONS, H. (1993): Strategies reproductrices des viperides dans les zones temperees fraiches et froides.- Bull. Soc. Zool. France; 117: 267-278.
- SAINT GIRONS, H. & KRAMER, E. (1963): Le cycle sexuel chez *Vipera berus* (L.) en montagne.- Revue Suisse Zool.; 70: 191-221.
- STILLE, B. & MADSEN, T. & NIKLASSON, M. (1986): Multiple paternity in the Adder, *Vipera berus*.- Oikos; 47: 173-175.
- STILLE, B. & NIKLASSON, M. & MADSEN, T. (1987): Within season multiple paternity in the Adder, *Vipera berus*: A reply.- Oikos; 49: 232-233.
- TINKLE, D. W. (1962): Reproductive potential and cycles in female *Crotalus atrox* from northwestern Texas.- Copeia; 1962: 306-313.

DATE OF SUBMISSION: October 28th, 1994

Corresponding editor: Heinz Grillitsch

AUTHORS: Dr. Massimo CAPULA, Dr. Ernesto FILIPPI, Dr. Luca LUISELLI, Department of Animal and Human Biology, University of Rome 'La Sapienza', via Alfonso Borelli 50, I-00161 Rome, Italy.

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Herpetozoa](#)

Jahr/Year: 1995

Band/Volume: [8_1_2](#)

Autor(en)/Author(s): Capula Massimo, Filippi Ernesto, Luiselli Luca M.

Artikel/Article: [Annual mating in female colubrid snakes with irregular reproductive frequency \(Squamata: Serpentes: Colubridae\). 11-15](#)