

NOTE BRÈVE

INDIVIDUAL REPRODUCTIVE SUCCESS AND CLUTCH SIZE OF A POPULATION OF THE SEMI-AQUATIC SNAKE *NATRIX TESSELLATA* FROM CENTRAL ITALY: ARE SMALLER MALES AND LARGER FEMALES ADVANTAGED?

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RÉSUMÉ. — *Succès reproducteur individuel et taille de ponte dans une population de la couleuvre semi-aquatique *Natrix tessellata* en Italie centrale : les plus petits mâles et les plus grandes femelles sont-ils avantagés ?* — Le succès de la formation des couples et de la reproduction de *Natrix tessellata*, serpent semi-aquatique, a été étudié dans le centre de l'Italie. Le succès des appariements a été établi en suivant par radiopistage 10 mâles et 12 femelles durant la période d'accouplement et en comptant combien chaque individu avait de partenaires sexuels en fonction de sa taille corporelle (longueur museau-anus). Les femelles étaient significativement plus grandes que les mâles. Deux patrons opposés de succès individuel ont été mis en évidence dans la population : un succès d'appariement plus grand pour les plus petits mâles et pour les plus grandes femelles. De fait, chez les mâles, il y avait une relation significative entre la taille du mâle et le nombre de femelles avec lesquelles il s'accouplait tandis que les plus grandes femelles étaient courtisées et s'accouplaient avec un plus grand nombre de mâles. La taille maternelle était positivement liée au nombre d'œufs pondus.

The Dice Snake (*Natrix tessellata*) is a semi-aquatic colubrid snake, widespread and locally very abundant along the Italian peninsula. With regard to the Italian populations, aspects of its field ecology have been studied in detail, particularly with regard to thermal ecology (Luiselli & Zimmermann, 1997) and feeding ecology (Luiselli & Rugiero, 1991; Filippi *et al.*, 1996). Its reproductive biology and mating success in the field are totally unknown, although it is reported that these snakes may reproduce annually in the Mediterranean bioclimates (Luiselli & Zimmermann, 1997), with oviposition period being in July, and hatching from mid to late August (Luiselli & Zimmermann, 1997). Concerning the mating season, very few information is available, but courtship and mating were reported to occur in water or in stream banks, often involving 3-5 males simultaneously courting single females (Luiselli & Zimmermann, 1997). According to Luiselli & Zimmermann (1997), mating of Mediterranean populations occur between mid April to early May, which is later than the mating season of sympatric Grass Snakes *Natrix natrix* (Luiselli, 1996).

In this note we report complementary data on the determinants of mating success and reproductive output of *Natrix tessellata* in a hilly locality of Mediterranean central Italy, in the hope to contribute to a better understanding of the reproductive strategies of this little

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known semi-aquatic snake. These data can be also of great value for comparisons with the mating strategies and reproductive biology of other Natricinae species (e.g. *Natrix natrix* and several species of the genus *Thamnophis*) which have become model organisms for this kind of studies in the recent international literature (Mason & Crews, 1985; Joy & Crews, 1988; Madsen & Shine, 1993; Luiselli, 1996).

MATERIALS AND METHODS

STUDY AREA

The field study was carried out at a hilly locality (valley of "Rio Fiume", Tolfa Mountains) situated about 60 km north of Rome (Latium, central Italy). This hilly area, with a elevation of about 250 m a.s.l., was characterized by a stream, with clear waters and stones on the banks, with a water depth of 30 cm to 110 cm, depending on the season. During summer, much of this stream dried up, and the Dice Snakes tended to be concentrated in just a few ponds which were formed along the stream bed. The gravid females were then observed mainly in the parts of the stream bed which were much rich of deep water (depth > 50 cm). The climate of the study area was Mediterranean-temperate, with cold winters (usually without snow), rainy spring and autumn, and dry and hot summer (hypomesaxeric subregion [type B] according to Tomaselli *et al.*, 1973).

PROTOCOL

The field study was conducted along this stream in different periods. To get data on individual mating success, we captured during the months of September–October 1992, several females and males. Thirteen males and seventeen females were anaesthetized, and then implanted with internal radiotransmitters (see Angelici *et al.*, 2000, for a synthesis of the method employed — although for the present case much smaller transmitters were employed than in the above-mentioned paper), and then set free at the capture point after a recovery period of 7 to 12 days. The transmitters were encapsulated in polyethylene and abdominally implanted. Each transmitter weighed approximately 2.5 g. Transmitters operated within the 171 MHz frequency range. The receiver CUSTOM CE-12, connected to a 4-elements Yagi antenna, was used; it received signals within approximately 100–200 m range. By the next spring, the various snakes were tracked to monitor their eventual mating activities, other than displacements and other eco-ethological data. Considering that these snakes are only diurnal during the spring months because of cold evenings and nights (Luiselli *et al.*, unpublished data), we concentrated every day field effort only between 6 a.m. and 6 p.m. Three males and five females were not tracked because they disappeared before the beginning of our spring study. It is not known whether these animals died or just moved away, but we suppose the latter hypothesis is more likely because we later (Summer, 1993) recaptured two females which were just emigrated from the study transect of respectively 535 and 779 m, and could not be tracked by our equipment. The remaining individuals were more sedentary, and were successfully tracked without major problems.

Females with eggs were opportunistically captured at the same study area between 1991 and 1999, and palpated in the abdomen to get data on their clutch size. To verify the reliability of this method with this species, we palpated five gravid females in the field and recorded their number of eggs, and then placed them in captivity until the oviposition occurred. By this procedure, we confirmed that in 4 out of 5 cases the exact number of laid eggs was also detected by abdominal palpation, whereas in a single case (relative to a large female) we estimated by palpation the presence of 31 eggs, but the female deposited just 29 eggs. In this later case, however, we could not exclude that two undetected eggs were retained by the female for some unknown reason, and that they were going to be deposited later after this specimen was released.

All snakes were measured for snout-vent length (SVL) to the nearest ± 1 mm, weighed to the nearest ± 1 g on an electronic balance, and individually marked by ventral scale clipping for future identification.

All statistical analyses were done with a STATISTICA (version 6.0) for Windows package, with alpha set at 5%, and all tests being two tailed.

RESULTS

Male and female mating success was studied in ten males and twelve females which were radiotracked during the mating season of 1993. In this sample, the females were significantly larger than the males (females: $\bar{x} = 70.2 \pm 10.7$ cm SVL; range 55.4 to 88.3 cm; males: $\bar{x} = 54.0 \pm 5.3$ cm SVL; range 48.5 to 63.0 cm SVL; $P = 0.0003$ at Student t-test with $df = 20$). In males, there was a significant negative relationship between male size (snout-vent-length, in cm) and number of females mated with ($r = -0.58$, $n = 10$, $P = 0.022$) (Fig. 1). In females, the opposite trend was detected, as the larger females were courted and mated with by a higher number of males ($r = 0.64$, $n = 12$, $P < 0.01$) (Fig. 2). Thus, two contrasting patterns of individual success were documented in this population: a greater mating success for smaller males, and for larger females.

Maternal-size (snout-vent-length, in cm) was positively related to the number of eggs produced ($r = 0.94$, $n = 21$, $P < 0.00001$) (Fig. 3).

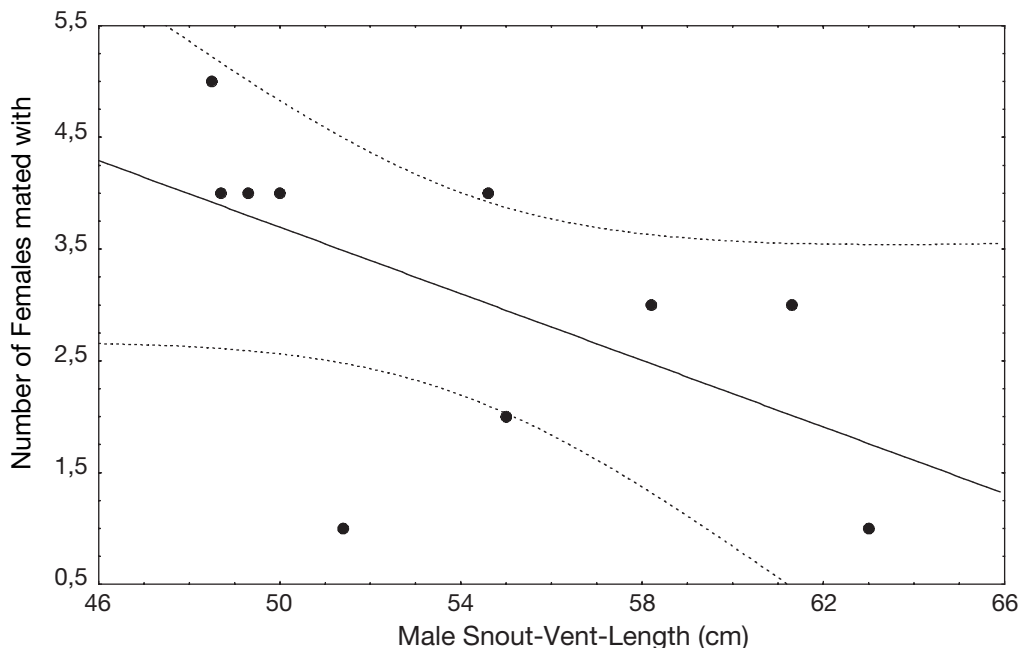


Figure 1. — Mating success in male *Natrix tessellata* from the study area, as expressed from the number of females mated with, in relation to male body size (SVL, in cm). Note that, the smaller is the male, the higher is the number of females mated with. For statistical details, see the text.

DISCUSSION

Our study is based unfortunately on a relatively small sample, and so the validity of our data need to be validated by further studies based on more adequate sample sizes. However, although limited, our data indicated some noteworthy patterns. With regard to females, both the higher mating success of large females (= higher number of courting males) and the higher number of eggs produced by larger individuals (= Darwin's fecundity advantage model) are consistent with the patterns observed in the better studied, closely related *Natrix natrix* (Madsen, 1983, 1987; Luiselli, 1996, Luiselli *et al.*, 1997). In this latter species it was indeed demonstrated that the larger females were always preferred by males when a choice between two differently-sized females was available (Luiselli, 1996), and also that clutch- and maternal-size were significantly positively correlated (Luiselli *et al.*, 1997). Thus, it is likely that the same patterns apply also to *Natrix tessellata*. Concerning the relationships between maternal- and clutch-size, it should be mentioned that these variables are often positively correlated in oviparous snake species (Naulleau, 1992; Shine & Madsen, 1997; Luiselli & Angelici, 2000; Santos & Llorente, 2001; Luiselli & Akani, 2002), although the strength of these relationships can be influenced by external proximate factors (for instance, prey availability), as well as by the type of reproductive strategy employed ("capital" versus "income" breeders, see Drent & Daans, 1980; Bonnet *et al.*, 2001). On the other hand, the pattern of individual mating success exhibited by male *Natrix tessellata* is very different from that of male *Natrix natrix*, because in the former species it seems that the smaller males are at an advantage (this study), whereas the

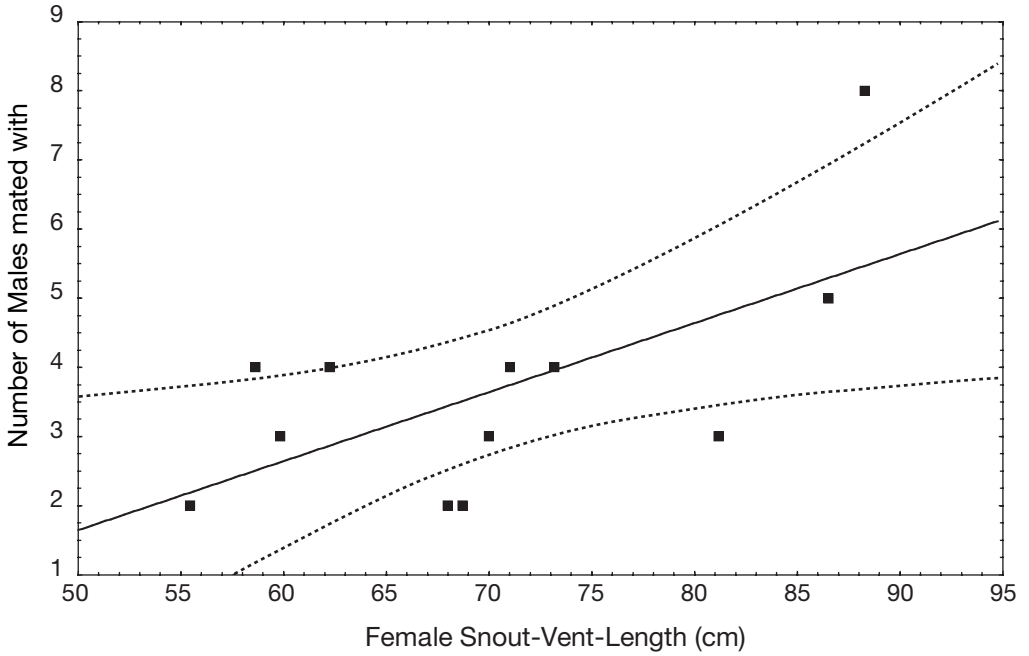


Figure 2. — Mating success in female *Natrix tessellata* from the study area, as expressed from the number of males mated with, in relation to female body size (SVL, in cm). Note that, the smaller is the female, the lesser is the number of males mated with. For statistical details, see the text.

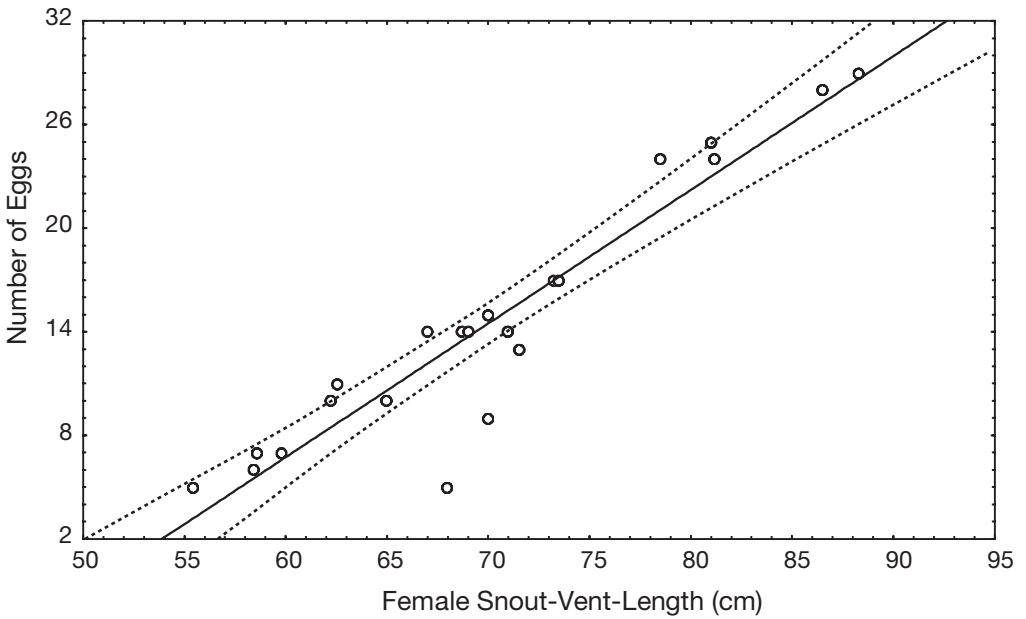


Figure 3.— Relationships between female snout-vent-length (cm) and number of eggs in *Natrix tessellata* from the study area.

opposite appears for the Grass Snakes (Madsen & Shine, 1993; Luiselli, 1996). Assuming that the data presented in this study are real and not just biased by the too small sample size, what does this pattern mean? Tentatively, we may suggest that smaller males are advantaged over larger males because the mating of *Natrix tessellata* often occurs in water (Luiselli & Zimmermann, 1997; Luiselli & Rugiero, unpublished data), and so the smaller males may be more agile and effective at swimming around “escaping” females, and at mating attempts. In terms of adaptive hypothesis, it is perhaps that this “small male advantage” may explain why in this species there is such a great reversed sexual size dimorphism, with males being much smaller than females. Practically speaking, it is perhaps that smaller males are selectively advantaged, and so that smaller body size may be selected by sexual selection, whereas for females it is obvious that natural selection may select for larger body size because of the higher fecundity of larger females (Darwin, 1871), and sexual selection may convergently select for larger body size because of the mating success of larger females compared to smaller females.

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