The causes of intraspecific variation in sexual dimorphism in the common grass snake populations, *Natrix natrix* LINNAEUS, 1758 (Serpentes, Colubridae): Data from the South Western Poland

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Abstract. Sexual dimorphism is widespread in animals, including snakes, and has important implication in both ecology and behaviour. I studied a grass snake (*Natrix natrix*) population from "Stawy Milickie" nature reserve. Mean snout-vent length (SVL) for females was significantly greater than SVL for males, but males had proportionally longer tails. However, relative tail length (TL) in males decreased with increasing SVL whereas in females it was constant. Larger tails in males have frequently been associated with increasing mating success (e.g. tail wrestling behaviour between males). However, it is possible this is less important in the population that I studied; instead, male snakes can allocate more energy to body growth.

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I. INTRODUCTION

Sexual dimorphism in snakes has been frequently studied, especially in terms of body size, body mass, shape and other morphological traits (e.g. KMINIAK & KALUZ 1983; FERICHE et al. 1993; SHINE 1993). In snakes, females generally reach larger size than the males (SHINE 1993). However, the reverse trend is observed in species in which the males fight (SHINE 1978, 1993, 1994). Others factors leading to differences in body size between the sexes include: (i) Size dependence of reproductive costs (larger females can store more and/or larger eggs). (ii) Reaching maturity and producing offspring at an earlier age (and at smaller size) may be favored if the probability of reaching maturity is at all low. If the mortality rate is high, then there may be an advantage for an individual to mature at an earlier age. Thus, one possible explanation of female-biased sexual dimorphism is higher mortality in males (BROWN & WEATHERHEAD 1999). (iii) Because larger snakes typically eat larger prey (ARNOLD 1993) size differences between the sexes may result in reduced competition for food between them (SHINE 1993).

The ontogenetic development of such dimorphism has been studied less often. For example, in many snake species, males have proportionally longer tails than females (SHINE 1993) and this di-

morphism is even seen in hatchlings (KING et al. 1999). However, it is generally unknown whether these differences increase, decrease or remain the same during ontogeny. GREGORY (2004) investigated this question in a population of grass snake (*Natrix natrix* LINNAEUS, 1758) in England. However, the patterns of sexual dimorphism may vary geographically, especially in the widely distributed species, such as *N. natrix*. Such differences between populations may result either from phenotypic plasticity or from population-specific adaptations (LUISELLI et al. 1997). Here I document a different pattern of sexual dimorphism in *N. natrix* from that described by GREGORY (2004).

Most studies of the ecology of the grass snake have been concerned with populations from both Western Europe, ranging from north (MADSEN 1983, 1984, MADSEN & SHINE 1993a, b), to south (GENTILLI & ZUFFI 1995, LUISELLI 1996 LUISELLI et al., 1997). Eastern European populations of grass snakes are not as well studied (e.g. JUSZCZYK 1987, MERTENS 1995). The aim of this study was to investigate the population structure of the common grass snake in the southwest of Poland and the allometric pattern of tail growth in males and females.

II. MATERIALS AND METHODS

This work was carried out in the nature reserve "Stawy Milickie" (51°31'51'' N; 17°20'12'' E). This is a protected area, part of the Regional Park of the Barycz valley. The main habitats are large areas of woodlands and many fishing lakes. However, fishing is subject to a strict control in the park, due to the needs of the local fauna.

The research was carried out from May-September 2000 and 2001. Fieldwork was conducted on warm days, at least once every two week, usually more often (22 field days in 2000 and 24 in 2001; total 46 field days). Snakes were captured between 08:00 and 11:00 hrs and 16:00 and 18:00 hrs, since they were most active in these periods. However, surveys were also conducted at other parts of the day.

Snout-vent length (SVL) and tail length (TL) were measured to the closest of millimeter. Snakes longer than 30 cm were marked by scale clipping (BORCZYK 1999). To avoid the risk of hurting small snakes individuals shorter than 30 cm were not marked. In addition in young, rapidly growing individuals these marks generally disappear after a few weeks (MADSEN 1983).

Because the data did not meet the ANOVAs assumption the differences in body length and relative tail length were analyzed using a Kruskall-Wallis test. Sexual Size Dimorphism (SSD) was determined using the standard formula, $x_l/x_s - 1$, where the x_l denotes mean length of the larger sex and x_s the mean length of the smaller sex (SHINE 1993). Thus SSD takes positive values when females are larger, and negative values when males are larger (SHINE 1993). The relationship between SVL and TL was expressed as linear regression of log(TL) on log(SVL). ANCOVA was used to compare the log(TL) between the sexes with log(SVL) as a covariate (i.e. relative TL after adjusting for SVL). Allometry of TL with respect to SVL was assessed by testing whether the slope of the regression was significantly different from 1 (see GREGORY 2004).

III. RESULTS

A total of 106 grass snakes (51 males, 41 females and 14 of unknown sex) were captured, marked and measured. The sex ratio was not statistically different from 1:1 ($\chi_{21} = 1.28$, P<0.297). Eight snakes had damaged tails and were omitted for the purposes of analyzing the tail length.

The distribution of SVL was normal for males (P = 0.25) and asymmetric for females (P=0.01). There was a statistically significant differences (P<0.0001) in the average SVL of males and females (males: median = 54.0, interquartile range = 48.0-59.0, range 32.5-70.0; females: median = 72.5, in-

terquartile range = 67.0-75.5, range 36.0-88.0; Fig. 1) and the SSD index was 0.31. The tail length was strongly correlated with body length (males r = 0.89, P = 0.001; females r = 0.93, P = 0.008).

Tail growth of females in relation to SVL was isometric (b = 0.9922, r^2 = 0.69, P>0.1), while the relative length of males tail declined with body size (b = 0.7714, r^2 = 0.72, P<0.005; Fig. 2). The difference between the slopes was statistically significant (P<0.0001). Because the slopes are different, the ANCOVA should be taken with caution. However, the Figure 2 shows that males have relatively longer tails than females at any SVLs which alleviates the difficulty of heterogeneous slopes.
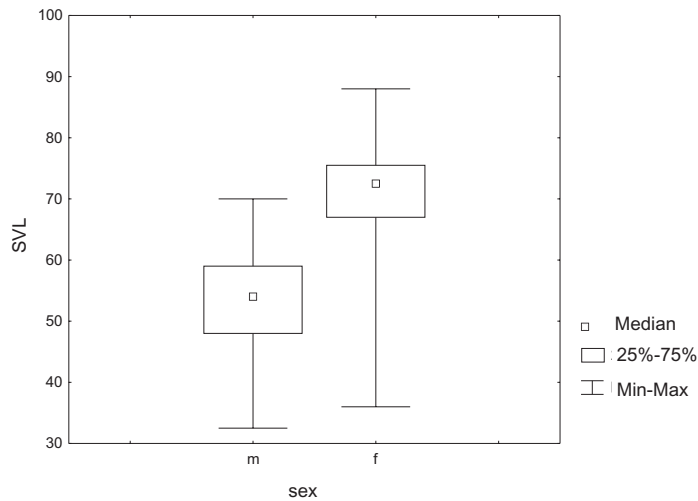

Fig. 1. The median, quartiles and ranges of the male and females SVL in the studied population of *Natrix natrix*.
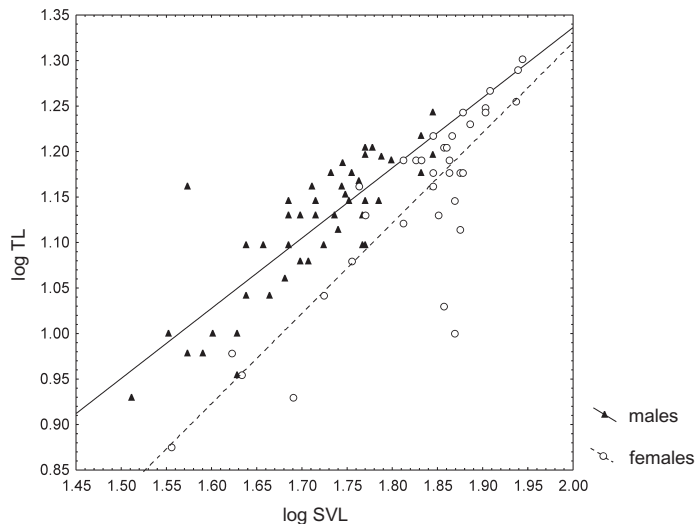

Fig. 2. The linear regression of the log-transformed tail length (logTL) on the log-transformed snout-vent length (logSVL) of males and females in the studied population of *Natrix natrix*. The female tails show isometric growth pattern in respect to the SVL, whereas male tales show negative allometry. However, males have relative longer tails than females at any SVLs.

IV. DISCUSSSION

I have observed male combat in my study population (BORCZYK 2004a), and because it is a general trend among snake species that exhibit male-combat that males are the larger sex (SHINE 1978, 1994), one might expect male-biased SSD. However, females are nonetheless the larger sex. Thus it is possible, that male combat does not play an important role in mating in this species, particularly because such behaviour was not reported from other populations of this species. The anurans (mainly *Rana* and *Bufo*) which are the main prey for grass snakes, are very common in the study area, and thus the food niche divergence should not be a factor driving the evolution of sexual size dimorphism in this case. In the study area, there is a wide range of potential predators (e.g. kites, ravens, storks, martens, foxes) that may hunt snakes (DYRCZ et al. 1991, BORCZYK, personal observation) Many snakes in the study population show signs of unsuccessful attacks by predators, and many snakes are also killed on the local road (BORCZYK 2004b). BONNET et al. (1999) suggest that mortality on roads may increase the reproductive costs incurred by snakes by a significant factor. Males often fall victim to road accidents when searching for females in the mating season. However, the data are insufficient to show how mortality (natural predator induced or road mortality) affects the sexual size dimorphism.

Why do male snakes have relatively longer tails than females? One suggestion is that a longer tail gives a male an advantage in mating (KING 1989). For example, in species with tail wrestling behavior, a long tail may increase the likelihood of copulation: the male with the strongest tail is able to push his rivals away and copulate with the female (the "male mating ability" hypothesis; KING 1989). However, the minimal length of the male's tail may also be limited by the copulatory organs' need for space at the tail's base (the "morphological constraint hypothesis"; KING 1989). Either way, males have proportionally longer tails than females. This difference can be observed just after birth (KING et al. 1999). Relatively shorter tails in females may be a result of selection favouring a large body cavity, which leads to an increase volume (the female reproductive output" hypothesis; KING 1989). The reproductive advantages of longer tails for males and of large body size for females suggest that dimorphism in the relative length of tails between the sexes should increase during the course of ontogeny. KING et al. (1999) noted that such changes occur in 3 of the 4 snake species they investigated. However, GREGORY (2004) found that tail length in small and large grass snakes was relatively constant; thus the tail growth was isometric with respect to SVL. In the population I studied, isometry was observed only in females. Differences between populations can result from a different system (e.g. resulting from snake density, length of mating periods, sex ratio), but the data are insufficient to draw conclusion on this point; both the present sample and that of GREGORY (2004) are rather small.

In my study population, larger males have proportionally shorter tails relative to smaller males. Thus, tail growth in males is negatively allometric. If the relative length of the tail were an important determinant of reproductive success, one would expect a greater allocation of resources to tail growth and, as a result, positive allometric growth. In contrast to SHINE et al. (1999), who supported both the "morphological constraint" and the "male mating ability" hypotheses for relative tail length of males, I suggest that the main force leading to longer tails in males is the necessity to provide space for the hemipenes and associated musculature – the "morphological constraint" hypothesis. In snake species in which tail wresting behaviour and mating balls do not occur (e.g. Viperidae, some Colubridae) males have longer tails relative to females (e.g. FERICHE et al. 1993, SCALI & GENTILLI 1998) which speaks in favour of the "morphological constraint" hypothesis. Of course, presence of tail wrestling behaviour could be an additional factor increasing these differences. See also MADSEN & SHINE (1993a) and LUISELLI (1996) for discussion of the importance of body length and tail length for success in mating balls. Further studies on this subject are needed and should cover a greater diversity of snake species, paying special attention to intraspecific variability and reproductive strategies in different populations.

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