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INDIVIDUAL GROWTH RATES OF NIKOLSKY'S VIPER, *VIPERA BERUS NIKOLSKII* (SQUAMATA, VIPERIDAE)

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Individual Growth Rates of Nikolsky's Viper, *Vipera berus nikolskii* (Squamata, Viperidae). Bondarenko, Z. S., Zinenko, O. I. — Capture-mark-recapture data was used to infer growth rates of the Nikolsky's viper, *Vipera berus nikolskii* (Vedmederja, Grubant et Rudaeva, 1986), in the Eastern Ukraine. We have found that growth rate is negatively correlated with age. The difference in growth rates before maturation is not significant between different sexes. Growth rates decrease rapidly after maturation in males and females, however adult males retain significantly higher average growth rates. There is large dispersion of growth rates in the group of adult females, which is caused, probably, by alteration of complete arrest of growth in the years with reproduction and more intensive growth in the years without it. Asymptotic snout-ventral length estimated after Von Bertalanffy model was 680 mm in females and 630 mm in males. Females mature after fifth and males mature after fourth hibernation. The larger females in vipers can not be the result of higher growth rates in females, but are the outcome of a combination of other factors including different maturation time and size (older and being larger), and, perhaps, longer life span due to lower mortality. Growth rates of the Nikolsky's viper in the nature are higher than in other species in the group of small Eurasian vipers.

Key words: growth, snakes, von Bertalanffy model, asymptotic size, capture mark recapture, sexual dimorphism.

Introduction

Growth rates and its dynamics during ontogenesis is an important characteristic which predicts many ecological and demographic parameters of organisms, populations and species. In vipers the connection has been documented between growth rates, longevity and mortality (Baron et al., 2010; Forsman, 1992; Madsen, 1988; Madsen, Stille, 1988), maturation age and fecundity of females (Bonnet et al., 2003; Capula et al., 1992), and accessibility of large prey (Forsman, 1992). Growth rates in the common adder *Vipera berus* (Linnaeus, 1758) are found to be dependant from environment (Forsman, 1993; Lindell, 1997), mainly from climatic factors.

Individual growth rates in vipers in Eastern Europe were studied several times (Grubant et al., 1973; Kheruvimov et al., 1977; Pavlov, 1998; Tabachishina et al., 2003), but model approach was never applied and there is no data from natural populations of Nikolsky's viper, *Vipera berus nikolskii* (Vedmederja et al., 1986). It is a subspecies of the common adder *V. berus* and a sister taxon to Turkish Baran's viper from the common adder complex, *Vipera barani* Böhme et Joger, 1984 (Kalyabina-Hauf et al., 2004). Nikolsky's viper is a relic that differentiated in forest refugia of Eastern Europe, on the southern border of the common adder's complex range (Milto, Zinenko, 2005). Depending on adopted species concept, Nikolsky's viper could be treated as a separate species or, if to take into account a wide introgression zone, as a subspecies of the common adder *Vipera berus* (Linnaeus, 1758) (Milto, Zinenko, 2005; Zinenko et al., 2010).

The aim of the current work is to study individual growth rates of different age and sex groups in the natural population of Nikolsky's viper. The results of this study could be used in the future to differentiate the influence of the climate and selection on maximal body size and sexual dimorphism in closely related species of small Eurasian vipers.

Material and methods

The material was collected between 1998 and 2008 years in the vicinities of biological station of V. N. Karazin Kharkiv University, Gaidary, Zmijiv District, Kharkiv Region, Ukraine. We collect vipers between March–April and in October. Snout-ventral length (SVL) and tail length were measured. Most of the snakes were caught just before or after hibernation, either at the end of September to the first half of October, or from April through the first ten days of May.

For the identification of individuals we use pictures of upper surface of a head, where the scalation pattern is unique, does not change during life and can be used for reliable recognition of recaptured specimens (Drobenkov, 1989). We register capture date, place, SVL and tail length, sex and physiological state (reproductive status, stage of moulting, feeding). All snakes were released in the capture place.

Due to expressed sexual dimorphism, ontogenetic and physiological differences, we divide snakes in four groups when characterizing growth rates: adult males, adult females, juvenile males and juvenile females. We consider adult snakes as animals with SVL larger than minimal size of observed reproducing individuals, over 400 mm in males and 540 mm in females (Zinenko and Bondarenko, unpublished data; Zinenko, 2006).

We define active periods as the time when snakes were actively feed according to our field observations. In males, the beginning of active period was identified by the end of mating period. The end of active period was the last observations of specimens with stomach content, proved by palpation or defecation. Thus, the active period in the group of adult males is 164 days long, between 5th of May and 15th of October, and in all other groups it is 184 days, between April, 15th and October, 15th (Zinenko and Bondarenko, unpublished data; Bea et al., 1992; Zinenko, 2006).

We applied the Von Bertalanffy (1) equation separately for males and females to build growth curve. Von Bertalanffy growth model was used in numerous papers dealing with growth rates of reptiles and performed better then logistic-by-length or logistic-by-mass models (James, 1991; Roitberg, Smirina; 2006; Zúñiga-Vega et al., 2008).

$$SVL_t = SVL_{birth} + SVL_{inf}(1 - e^{-Kt}),$$

where SVL_t is SVL at time t , measured in days of activity, SVL_{inf} — asymptotic SVL, K — characteristic growth parameter. The parameters SVL_{inf} and K were calculated from relation of growth rate and body size $dSVL/dt = K(SVL_{inf} - SVL)$ (Schoener and Schoener, 1978). The initial SVLs of newborns SVL_{birth} (males — 176.3 mm; females — 179.7 mm) were averaged from our data and are about size of newborns from the same population reported elsewhere (Zinenko and Bondarenko, unpublished data; Zinenko et al., 2005).

Since relationships between growth rates and SVL derived from Von Bertalanffy equation is a linear function $dSVL/dt = K(SVL_{inf} - SVL)$, which has all parameters of Von Bertalanffy equation itself (Schoener and Schoener, 1978), we fit this function to real dataset using linear regression in Statistica 6.0 similarly to (Zúñiga-Vega et al., 2008). Then we used K and SVL_{inf} values to build growth curves and compared observed individual growth trajectories with the curve by plotting them on the same graph.

We perform test of normality to the growth rates in four groups (adult males, adult females, juvenile males and juvenile females) and compare normally distributed parameters using Student's t -test, or nonparametric Mann-Whitney U -test if distribution of the parameters deviated from normal. We also use conservative approach and treated differences between parameters of Von Bertalanffy model as different if their 95 % confident intervals (CI) did not overlap (Schoener and Schoener, 1978).

Results

We recapture 19 males and 16 females. A number of specimens were encountered more than twice in a course of study, thus we had 27 recaptures for males and 23 recaptures for females. Most of the recaptures happened within one (58 %), two (26 %), or three or more (16 %) seasons. The same specimen was observed maximally across five years.

Growth rates in different sex and age groups are presented in table 1. All groups, except of adult females, had normal distribution of growth rates. Mean growth rates were significantly different between groups of adult and juvenile specimens ($p = 0.004$ and $p = 0.0015$ in males and females, table 1). In the contrary, the difference between groups of different sexes of juveniles was insignificant ($p = 0.49$). Adult males grow faster than females ($p = 0.008$), but the range of growth rate in females is higher. The minimal and maximal growth rates in females were lower (0 mm/day) and higher (0.714 mm/day) than in adult males group (0.061–0.552 mm/day).

Both males and females demonstrated strong negative correlation between growth rates and SVL ($r_2 = 0.44$, $p < 0.001$) (fig. 1). Large variation in growth rates was observed in males of 300–450 mm (range 0.07–0.82 mm/day) and females around 400 mm SVL (range 0.14–1 mm/day).

We identified the parameters of the theoretical Von Bertalanffy curve for males as $SVL_{inf} = 631.77$ (CI : 560.1–811.25) mm, $K = 0.0015 \pm 0.0003$ and females $SVL_{inf} = 679.55$ (CI : 609.5–856.0) mm, $K = 0.0017 \pm 0.0004$. Since 95 % confidence intervals are broadly overlapping in both parameters, the differences between them are not significant according to conservative approach (Schoener and Schoener, 1978).

Table 1. Growth rates in different sex and age groups of *V. b. nikolskii*, mm/day

Data	Juveniles, females	Adult, females	Juveniles, males	Adult, males
Number of observations	8	15	9	18
Mean ± Standard Error	0.502 ± 0.093	0.136 ± 0.047	0.414 ± 0.083	0.247 ± 0.035
Minimum–Maximum	0.138–0.993	0.00–0.714	0.067–0.820	0.061–0.552
Shapiro–Wilk's W-test of normality	W = 0.952, p = 0.727	W = 0.705, p = 0.000	W = 0.976, p = 0.939	W = 0.921, p = 0.132

Observed individual growth trajectories match satisfactory the theoretical Von Bertalanffy curve for both sexes (fig. 2). The most intensive growth, both in males and females, is typical for the beginning of life and ends with maturation. An inflection point of individual growth rates happens approximately at the SVL 400–600 mm and coincides with the beginning of reproduction. Growth rates decreases stronger in females compared to males and it can be seen on coefficient K of Von Bertalanffy equation, however asymptotic SVL for females are larger than for males.

Quite often we observed zero growth in adult females (for example female No 63 was measured 700 mm both in autumn 2001 and spring 2004). At the same time, the same animal earlier demonstrated high growth rates and exceeds the mean theoretically predicted SVL_{inf} when during 2001 season added 110 mm to SVL 590 mm and reached 700 mm.

Discussion

V. b. nikolskii has higher growth rates before sexual maturation, which agrees with literature data on observation of other vipers (Korosov, 2010; Madsen, 1988; Tabachishina et al., 2003; Volsoe, 1944) which are also predicted by Von Bertalanffy equation. Similarity in the growth rates between juvenile males and females (table 1) agree with published results (Baron et al., 2010; Forsman, 1993); however, there is insignificant tendency of higher growth rates in females. The correlation between growth rates and number of vertebra or ventral scales in *V. berus* is documented (Lindell et al., 1993; Lindell, 1996). Since females *V. b. nikolskii* have more ventral scales than males (Mילו, Zinenko, 2005) it can be one of the factors which explains this bias to a slightly higher growth speed in juvenile females, however higher growth rates of females is still to be supported by additional data and the tie between growth rates and sex associated anatomy is to be proved by more observations. Slightly different mean initial newborn SVL in males and females (the difference between which comprise 3.4 mm, less than 2 % of SVL — Zinenko et al., 2005) have minor influence on calculated growth curve. According to Von Bertalanffy equation such small difference could be compensated by 3 days of growth. Taking into account natural fluctuations of growth pattern due to prey availability

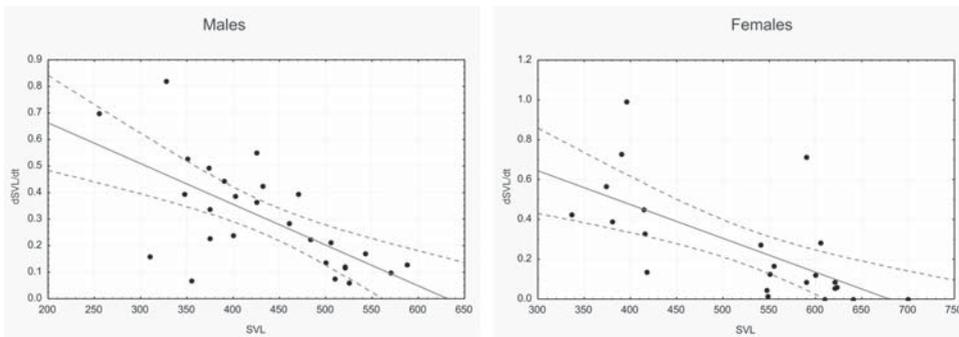


Fig. 1. Relationship between growth rates (dSVL/dt) and snout-ventral length (SVL) in males and females of *V. b. nikolskii*. Dashed lines show 95 % confidence intervals of the expected theoretical curve.

and weather, the effect of initial size could be neglected. Additionally in real snakes the ranges of SVL variation in newborns of both sexes are broadly overlapping (Zinenko and Bondarenko, unpublished data; Zinenko et al., 2005). Slightly different initial newborn SVL in males and females seems to have a minor influence on the calculated growth curve.

A large extent of individual variation in growth rates has been observed in the common adder (Kheruvimov et al., 1977). In our dataset a large dispersion of growth rates (fig. 1; table 1) could be seen in the group of smaller animals (fig. 1). This may be caused by discrete and rare feedings on large prey. Nikolsky's viper almost exclusively feeds on small mammals. In our study site, the diet is composed of voles (Zinenko, unpublished data; Zinenko, 2006). Comparatively large body size in prey objects and high efficiency of assimilation (Pomialovska-Pilipiuk, 1974) influence the smoothness of the growth curve, with more intensive growth associated with successful feeding episodes.

In females dataset all snakes are forming two groups — juveniles and adults, but there is a gap corresponding to transition SVL between them (fig. 1). We also observed this phenomenon on SVL data in various populations of different reptiles, when frequency of animals of transitional size in the population census drops down comparing to neighbour classes of juveniles and adults (Zinenko, 2006). Putative explanation of this fact may be in continuous decrease of number of individuals in size class due to mortality and growth. After attaining maturation size and beginning of the reproduction adults became more exposed due to changes in activity pattern and therefore their apparent abundance grows again.

Adult females in average grow slower than males. According to individual growth trajectories differences in growth rates in different years are most prominent in this group. Several adult females demonstrated both very high rates of growth and complete arrest of growth (fig. 1, 2; table 1), usually associated with reproductive status. Gravid snakes did not grow in the year of reproduction. Nikolsky's vipers, like other vipers, is a typical "capital breeder" and developing embryos are maintained by inner reserves, accumulated earlier in life (Bonnet et al., 1998). Therefore, high investments in reproduction make smooth growth of females impossible. Recovery and further accumulation of resources may also hamper growth in the first year after reproduction, but in our dataset there are no observations that span consecutive years after reproduction to definitively show this.

According to our observations, both periods of intensive and slow individual growth of adult females may last more than one season. Such alteration of growth versus reproduction in biennial or triennial reproduction cycles in females *Vipera ursinii* Bonaparte, 1835 is well known (Baron et al., 2013). Thus, Von Bertalanffy equation is a good approximation to averaged long term growth of adult females, which summarizes growth rates of biennial or longer

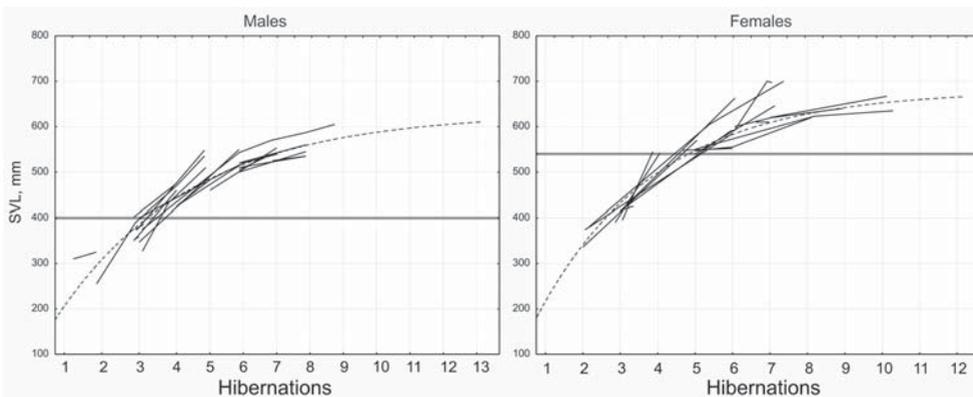


Fig. 2. Individual growth curves of males and females of *V. b. nikolskii* approximated with the Von Bertalanffy growth curves. Solid lines connect observed SVL of recaptured specimens. Dashed lines represent the Von Bertalanffy growth curve. Horizontal solid line is the size of maturation. X-axis measures time in days, hibernations are indicated by numbers. The duration of active period before first hibernation was assumed to be 45 days; all consecutive active periods lasted 184 days, except for 164 days in adult males.

reproductive cycle, but does not match individual growth trajectories within one particular season. It does not imply alterations of reproductive and barren years, which lead to heterogeneity of growth rates in adult females and their non normal distribution of growth rates.

The overlap of confidence intervals of the growth parameter K and estimated asymptotic size SVL_{inf} are making differences between Von Bertalanffy growth curves of males and females not significant. We believe that this criterion of significance is too conservative. It contrasts with the results of direct test of growth rates in different sex and age groups. The broad ranges of 95 % confidence intervals comes from high variation of individual growth rates and low number of observations.

The Von Bertalanffy curve allowed us to infer the maturation age in the Nikolsky's viper. The curve crosses the minimum size of reproduction by the fourth hibernation in males and the fifth hibernation in females. Sexual size dimorphism in *V. b. nikolskii* is female-biased; adult females on average are 64 mm longer than males (Milto, Zinenko, 2005). This difference approximately corresponds to seasonal SVL change and also almost matches the 50 mm difference in SVL_{inf} between males and females. Thus, the difference in maturation size and time, but not growth rate, is our explanation of sexual dimorphism in vipers. Additionally, bias towards larger females in populations could be introduced by higher mortality and shorter lifespan in males; however, we could not measure these factors in this work. According to our observations, we can only identify the maximal observed age in females as 10 hibernations (two specimens) and in males as 8 hibernations (7 years) (fig. 2).

V. b. nikolskii has high growth rate of 0.7–0.85 mm/day compared to closely related species of small Eurasian vipers, especially in young specimens (Tabachishina et al., 2003; Korosov, 2010). Maximum growth rate of individuals of Nikolsky's viper in captivity was 430–470 mm in one year (1.18–1.29 mm/day) and were observed in laboratory conditions under intensive feeding and high temperature (Grubant et al., 1973), but these rates are not applicable to snakes from nature. In a more realistic experiment in the laboratory, snakes from Tatarstan (*V. b. berus*) had also quite high growth rates during first 20 month of life (0.8 mm/day — Pavlov, 1998), but lower than in the conditions from previous paper. The highest growth rates in the Nikolsky's viper may be the direct outcome of its' southern range and prevalence of larger prey in the diet. Alternatively, larger newborns in this subspecies (Zinenko et al., 2005) could be connected with stronger selection towards larger females, which could be attained by genetically controlled higher growth rates (Grubant et al., 1973).

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