ZooNotes 299: 1-4 (2026)
www.zoonotes.bio.uni-plovdiv.bg
ISSN 1313-9916
DOI: 10.69085/zn20260299

Prey type influences predator–prey size relationship in *Natrix natrix* (Linnaeus, 1758) (Reptilia: Colubridae)

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Abstract: In the current study the relationship between predator body length and prey body length in the Grass Snake (*Natrix natrix*) is examined, based on data from 39 individuals collected in the city of Plovdiv, Bulgaria. Prey items were classified into two categories - "fish" and "frog". A significant positive relationship between snake length and prey length was registered, indicating size-mediated prey selection. The scaling relationship was stronger in snakes consuming frogs than in those consuming fish. Relative prey size differed significantly between prey types, with fish representing proportionally larger prey.

Key words: Predator-prey, prey selection, trophic interactions.

Introduction

Predator-prey body size relationships take a very important part of trophic ecology, profoundly shaping prey selection, handling capabilities, and energy gains in vertebrate predators (Jackson et al. 2004, Hampton 2018). For snakes, predator size imposes key limits on the maximum and minimum ingestible prey sizes, driven by morphological and functional constraints in their feeding capabilities. Moreover, many snake species exhibit ontogenetic, size-dependent dietary shifts associated with changes in body size and feeding performance (Luiselli *et al.* 1997; Hampton 2018).

The Grass Snake *Natrix natrix* (Linnaeus, 1758) is a widespread semi-aquatic colubrid snake distributed throughout most of Europe (including Bulgaria) and parts of western Asia (Stojanov *et al.* 2011). The species is considered a generalist predator that feeds primarily on amphibians and fish, although other vertebrates may occasionally be consumed (Luiselli *et al.* 1997, Gregory & Isaac 2004).

Previous studies have shown that prey size in *N. natrix* correlates strongly with predator body size, driven by morphological limits and ontogenetic shifts in feeding ecology (Luiselli et al. 1997, Gregory & Isaac 2004). Larger snakes can typically capture and swallow bigger prey, leading to changes in prey composition and relative prey size.
Despite numerous studies into *N. natrix* feeding ecology, quantitative assessments of predator-prey size relationships are still scarce. The aim of the present study is to examine the relationship between body length of *N. natrix* and the body length of consumed prey, and to compare size-scaling patterns between two major prey categories - fish and frogs.

Material and Methods

The material used in the current study was collected in 21-28.08.1974 by the late Assoc. Prof. Atanas Donev†, PhD from the State Fishery (now Institute of Fisheries and Aquaculture) in the city of Plovdiv, and the data (previously unpublished) kept in the Department of Zoology, Faculty of Biology at the University of Plovdiv "Paisii Hilendarski". The total of 40 Grass snakes were captured and their stomach contents extracted, by Assoc.

Received: 08.03.2026
Published: 28.05.2026
Университетско издателство "Паисий Хилендарски"
Plovdiv University Press "Paisii Hilendarski"

Prof. Donev†. The prey wasn't determined taxonomically, rather just the prey type, categorised in two categories - "fish" and "frog". The collected data consisted of body length of the snakes (L.snakes), body length of the consumed fish (L.fish) and body length of the consumed frogs (L.frog). All measurements given in centimeters.

Relative prey size was calculated as the ratio between prey body length and predator body length (L.prey/L.snake), following standard methodology used in predator–prey size relationship studies (Jackson *et al.* 2004, Hampton 2018).

All statistical analyses were performed using software "PAST" v.5.2 (Hammer *et al.* 2001). Due to non-normal distribution, the data was normalised via log10 transformation (Fowler *et al.* 1998). The association between snake body length (L.snake) and prey body length (L.prey) was analysed using Pearson linear correlation. Allometric relationships were examined by applying OLS regression to log10-transformed length measurements. The significance of the regression slope was evaluated using a t-test, and parameter robustness was assessed with 1,999 bootstrap replicates and a permutation test. Differences in body size between prey categories (fish vs. frogs) were tested using Mann-Whitney's U-test. From the z-value, the effect size was calculated: $r=z/\sqrt{N}$, where N is the total number of observations (fish + frogs) and *z* is the standardised test statistic from the Mann-Whitney's U-test, following Rosenthal (1991) and quantified following Cohen (1988).

Results and Discussion

From the examined snakes, one was with empty stomach and it is excluded from the analysis. A total of 24 snakes consumed fish and 15 consumed frogs. Descriptive statistics of the data is presented in Table 1.

Table 1. Descriptive statistics of the body length of the measured snakes (L.snake), fish (L.fish) and frogs (L.frog) in the current study. All measurements are in centimeters.

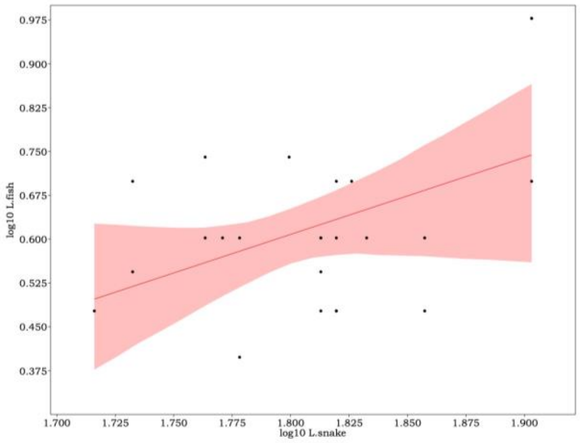
Parameter	L.snake	L.fish	L.frog
N	39	24	15
Min	43	2.5	1.5
Max	80	9.5	4.5
Mean	63.66667	4.395833	2.866667
Std. error	1.35043	0.3611314	0.2510296
Stand. dev	8.433434	1.769175	0.9722336
Median	63	4	2.5
Coeff. var	13.24623	40.24665	33.91512

There is a statistically significant moderately strong positive correlation between snake length and prey length (fish and frogs combined - $r=0.65$, $p=0.0000084$). The coefficient of determination ($r^2 = 0.42$) indicates that ~42% of the variation in prey length is explained by snake length.

Predator body length showed a significant positive relationship with prey length when only fish prey were considered (OLS regression: slope = 1.32 ± 0.53 SE, $t = 2.50$, $p = 0.020$; Fig. 1). The correlation coefficient was moderate ($r = 0.47$), explaining approximately 22% of the variance in prey size. Bootstrapped confidence intervals confirmed the positive slope (95% CI: 0.17–2.85).

In contrast, the relationship between snake length and frog length was considerably stronger. Regression analysis revealed a highly significant positive relationship (OLS regression: slope = 1.78 ± 0.36 SE, $t = 4.88$, $p = 0.0003$; Fig. 2) with a strong correlation ($r = 0.80$), indicating that predator size explained approximately 65% of the variation in frog size.

Bootstrapped confidence intervals for the slope remained entirely positive (95% CI: 1.35–2.26).



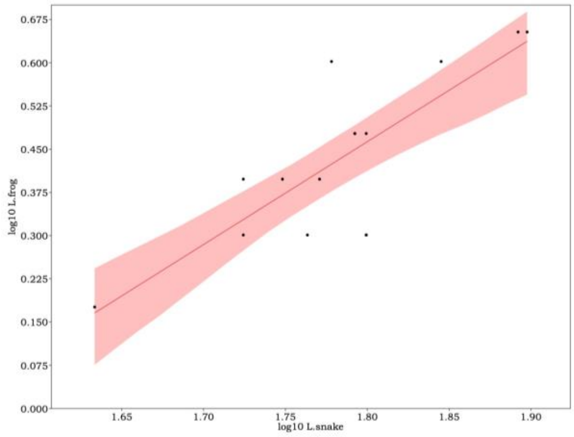


Fig. 1. Relationship between snake body length and fish prey length in *Natrix natrix*. The regression line indicates a significant positive relationship between predator and prey size.

Fig. 2. Relationship between snake body length and frog prey length in *Natrix natrix*. The strong positive correlation indicates pronounced size-dependent prey selection.

Relative prey size differed significantly between the consumed fish and frogs (Fig. 3). A Mann–Whitney test showed that fish represented proportionally larger prey than frogs (U = 60, z = 3.45, p = 0.00056). The calculated effect size (ES) based on the total number of observations (fish + frogs) is 0.55, which is interpreted as a large effect in similar ecological studies. This result is fully consistent with previous analyses - strong positive allometry was found for frogs, while the relationship for fish is weaker. Therefore, the Mann-Whitney test confirms that prey type is associated with a significant difference in relative size, supporting the hypothesis of size-mediated prey selection.

Linear regression analyses nevertheless revealed positive scaling between predator and prey size in both prey categories. The relationship was weaker in snakes consuming fish, but substantially stronger in snakes consuming frogs. Thus, although fish tended to represent relatively larger prey overall, the size of frogs consumed increased more strongly with snake body length. This indicates a tighter size matching between predator and prey in frog-feeding individuals.

For many snakes, predator and prey size are positively correlated, with larger snakes consuming larger prey (Kornilev *et al.* 2023). The strong positive relationship between snake body length and frog length registered in the present study is consistent with previous observations that amphibian prey size in *N. natrix* increases with predator size (Luiselli *et al.* 1997, Gregory & Isaac 2004, Hampton 2018). Larger individuals are capable of handling substantially larger anurans, which leads to clear ontogenetic scaling in predator-prey body size relationships.

The observed weaker correlation between snake length and fish length likely stems from variations in prey behavior and capture mechanics. Fish are typically caught in water, where their escape skills, body form, and swimming ability can affect prey availability regardless of the predator's size. Prey traits such as body size and defensive structures may be correlated, making it difficult to identify a single determining factor; for example, larger prey generally have greater body mass and more developed defensive structures (e.g. rough scales, horns, spines) (Kornilev *et al.* 2023). Consequently, size selection for fish may be less tightly constrained by the snake's morphology than for anurans. Notably, even with this looser scaling for fish, relative size metrics show that fish constitute proportionally larger prey than frogs. This enables snakes to swallow relatively large fish, unlike more sturdy amphibians of comparable length. Kornilev et al. (2023) describe in detail cases of mortality in *N. natrix* in attempts to consume prey, that is too large (both fish and frogs).

In conclusion, the findings support the idea of size-dependent prey selection in *N. natrix,* while revealing that the predator-prey size relationship varies across prey types. These variations likely arise from a mix of the snake's morphological limits, prey behaviors, and the habitat-specific abundance of different prey (Luiselli *et al.* 1997, Gregory & Isaac 2004, Hampton 2018, Kornilev *et al.* 2023).

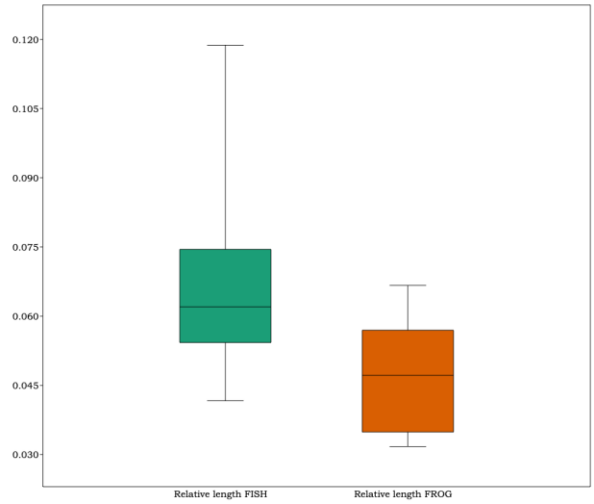


Fig. 3. Box & Whiskers plot of the relative size of the consumed prey by *N. natrix.*

Acknowledgements. The author is forever grateful to Assoc. Prof. Atanas Donev†, PhD (University of Plovdiv “Paisii Hilendarski”, Faculty of Biology, Department of Zoology) for the given data used in this study.

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