

Composition and scaling of male and female Alpine newt (*Mesotriton alpestris*) prey, with related site and seasonal effects

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In amphibians, most species are female-biased sexually dimorphic and such dimorphism is often accompanied by intersexual differences in prey composition. While many aspects of foraging ecology have been studied in this group, intersexual differences have rarely been described. We examined dietary composition of male and female Alpine newts (*Mesotriton alpestris*) from two localities in the Czech Republic during the entire breeding period by stomach flushing. Isopoda, Cladocera, *Rana* eggs were the most important prey. About 16% of newts did not contain prey items. At studied localities, females were about 15% larger than males. Snout–vent length (SVL) of newts was related to the mass of consumed prey, but not its number and diversity. Analyzing the residuals from the relationships between SVL and prey characteristics, we found the effect of sex on all observed prey variables — the females consumed more prey items, more diverse prey and also in greater mass than did the males.

Introduction

Sexual size dimorphism (SSD) is a common characteristic of many animal taxa (Darwin 1871, Andersson 1994). Male-biased sexual size dimorphism (MSSD), has been considered a product of male–male competition (Trivers 1972, Blanckenhorn 2005). SSD, however, can be also a consequence of intersexual resource partitioning (Shine 1989, Krüger 2005). In any case, the occurrence of SSD in particular species

should be accompanied by dietary differences between sexes, because varied resources would be used by individuals of different sizes (e.g., Shetty & Shine 2002, Zalewski 2007).

In fishes, snakes, raptors, owls and waders, females are usually the larger sex. In other reptiles, other birds and most mammals, males tend to be larger (Shine 1989, Andersson 1994, Krüger 2005, Vincent & Herrel 2007). FSSD has been reported in the majority of amphibians (Shine 1979), including newts from the genera

Lissotriton, *Mesotriton* and *Triturus* (Griffiths 1996, Malmgren & Thollesson 1999). While resource partitioning between morphs (Denoël & Andreone 2003, Denoël & Schabetsberger 2003, Denoël *et al.* 2004), interspecific competition (Fasola & Canova 1992, Joly & Giacoma 1992, Jehle *et al.* 2000), and feeding relationships of larval newts (Braz & Joly 1994, Griffiths *et al.* 1994, Babik 1998) are well known, the dietary differences between males and females have rarely been described, and even then generally only as a by-product of studies having a different focus (Joly & Giacoma 1992, Rulík 1993, Denoël & Demars 2008).

Because of newts' well-hidden lifestyle during their terrestrial phase (Verrell 1985, Schabetsberger *et al.* 2004), the majority of dietary studies were carried out during newts' breeding (aquatic) phase. Newts are prolonged breeders, remaining in the water for several months (Griffiths 1996, Arntzen 2002). During this time, environmental conditions, rate of intraspecific competition, as well as prey patterns and availability can change considerably (Griffiths 1997, Denoël & Demars 2008, Kopecký *et al.* 2010). To investigate potential intersexual dietary differences, one must examine the newts' entire breeding period. However, this approach has not always been taken (*see* Joly & Giacoma 1992, Jehle *et al.* 2000, Denoël & Schabetsberger 2003).

In newts, as in other animals (Beck *et al.* 2007), the larger sex may consume larger prey items or greater numbers of smaller prey items. Also, due to egg production, females may require more diverse food than males (Lewis *et al.* 2002). Hence, the principal aim of this study was to determine differences in prey scaling and prey composition (differences in prey mass, number of prey items, and number of prey categories) between sexes of the Alpine newt (*Mesotriton alpestris*) while controlling for the different body length of the sexes and possible changes in newts' foraging behavior across the entire aquatic period.

Materials and methods

Study sites

The study was conducted at two localities in

the Czech Republic near the town of Ledeč nad Sázavou. The first, hereafter referred to as locality A (49°42'45''N, 15°16'50''E; 452 m a.s.l.) is a fishless pond with a surface area of 36.0 m² and maximum depth of 0.8 m. The pond's banks are planted with willows (*Salix* sp.), and the pond is surrounded by pasture. The bottom is muddy and vegetation in the water is scant, consisting mainly of common duckweed (*Lemna minor*), starwort (*Callitriche verna*) and compact rush (*Juncus conglomeratus*). The pond is artificial, its original purpose being to drain water from surrounding wet plots. During the study, the water's pH ranged from 6.5 to 7.0.

The second locality, hereafter B (49°44'24''N, 15°16'59''E; 444 m a.s.l.), is a now fishless pond that was historically used for fish rearing. Pond B is situated in a spruce forest. It has a surface area of 27.5 m² and maximum depth of 0.3 m. The pond's bottom is muddy. Water plants, consisting mainly of the common waterweed (*Elodea canadensis*), starwort and reed managrace (*Glyceria aquatica*), cover a large part of the pond's surface area. During the study, pH values were around 5.5.

A small number of smooth newts (*Lissotriton vulgaris*) and common frogs (*Rana temporaria*) inhabited both ponds.

Sampling and diet analysis

Adult Alpine newts were captured by net from the shore at three time points representing their entire breeding season. Sampling was done during daylight hours in 1997: once in April, once in May and once in June. The newts were kept in a container filled with water from the pond and marked (Heyer *et al.* 1994) by toe-clipping (Ferner 1979) different for each date of capture. To avoid data dependence (Luiselli *et al.* 2007), only newts captured for the first time were used in the study. Each captured and unmarked newt was measured (snout-vent length, SVL) to the nearest 0.1 mm. The content of its stomach was extracted using a stomach flushing technique described by Opatrný (1980): 1 ml syringe with 80 mm hypodermic flexible needle with last 30 mm before the tip covered by plastic tubing was used. This terminal part of the needle was

gently inserted through mouth of the newt into the stomach and 1 ml of water was injected. Usually two and maximally three flushes were conducted. Measured and flushed newts were not anesthetized. Newts were released back into the water immediately after these procedures.

The stomach contents were individually stored in vials and preserved in 4% formaldehyde. Prey items were identified using a stereoscopic microscope and sorted into 19 taxonomic and four biomass categories — 0.001 g for Cladocera, Cyclopoida, Megaloptera larvae and Turbellaria; 0.01 g for Chironomidae larvae, Chironomidae pupae, Culicidae pupae, Bivalvia, Gastropoda, and Dytiscidae larvae; 0.1 g for Ephemeroptera larvae, Ephemeroptera pupae, Lepidoptera larvae, Plecoptera larvae, Trichoptera larvae, Arachnida, Isopoda, and *Rana* eggs; and 1 g for *Lumbricus* — due to the technical impossibility of weighing all (1417) prey items thus obtained. Categorization of prey taxa into prey categories was based on the previously published works (Opatrný 1968).

Sex of the newts was determined using external secondary sexual characters. Sexual size dimorphism was determined using the sexual dimorphism index (SDI) proposed by Lovich and Gibbons (1992):

$$\text{SDI} = (\text{size of larger sex} / \text{size of smaller sex}) \pm 1$$

[+1 if males are larger, -1 if females are larger].

The index of relative importance (IRI), and %IRI for each prey category (i), were computed, following Mariano-Jelicich *et al.* (2007), as:

$$\text{IRI}_i = f_i(n_i + m_i)$$

$$\% \text{IRI}_i = (\text{IRI}_i \times 100) / \text{IRI}_{\text{total}}$$

where f is the percentage of newts containing prey category i , n is the percentage of prey category i of all prey items, and m is the percentage of biomass of prey category i of the estimated total biomass consumed.

Statistics

Only newts which contained prey items were used in analyzing intersexual diet differences.

Newts containing only non-prey items like plants, algae and mud or which had completely empty stomachs were analyzed in a separate model.

We intended to compare sex ratio between localities across the entire sampling period (April–June). Since a non-significant result might be obtained even when the sex ratio is biased as long as sex ratios are the same across all months, we took into consideration the month of sampling as an additional variable. Hence, we used a generalized linear model with Poisson's distribution of the response variable (numbers of newts) and sex, locality, month and particularly the interactions between sex, month and locality as the explanatory variables. To obtain a minimal adequate model, we simplified the maximal model using a chi-squared deletion test (Crawley 2007).

We used the same statistical procedure for comparing newt numbers in relation to their replete status (replete *vs.* newts with empty stomachs), sex, locality, month and the interactions of these as the explanatory variables.

We wanted to distinguish intersexual diet differences from the pure effect of different body sizes between sexes. The first step was to determine SVL differences between males and females. To take into account possible variability in SVL between localities and within the long breeding period (from April to June), we analyzed the effects of sex, locality and month (including their interactions) on SVL of newts by linear model. Afterwards, we simplified the maximal model using an F -deletion test and by grouping indifferent factor levels for the sole variable having more than two levels (that being the factor month, with levels April, May and June) (Pekár & Brabec 2009).

Since the SVL of newts was significantly affected by all main factors (i.e. sex, locality and month), it was necessary to separate the effect of SVL from possible intersexual diet differences in the subsequent prey analyses. Hence, we made regression analyses of prey variables (separately for prey mass, prey categories, and number of prey items) on SVL of newts. The residuals obtained, in fact representing unexplained variability from these relationships, were used as the response variables in the models analyzing the effects of sex, locality and month on particular prey variables.

Due to heftiness and to avoid its possibly affecting our study, we did not measure the prey availability in the ponds, which could have been different between the two localities and also could have changed over time. To exclude effects of location- and time-related differences in prey availability, we created a new variable called “population,” containing only newts from the same locality and identical time of sampling (i.e. from the same month). The assignment of newts to a particular population was included in linear mixed-effects models as the explanatory factor with random effect. Thus, the effect of sex (explanatory variable with fixed effect) was analyzed only within these populations. Such model was separately calculated for each prey variable (i.e. prey mass, prey categories, and number of prey items). During the following model simplification, we first tested interactions between fixed and random effects using a chi-squared test, and then we compared models with and without the variable ‘sex’ using ANOVA and a maximum likelihood method (Crawley 2007).

The threshold for statistical significance was set at $\alpha = 0.05$. At the end, each minimal adequate model was checked using standard statistical diagnostics, i.e. by residuals and standardized residuals *versus* fitted and predicted values and by Cook’s distances (Crawley 2007, Pekár & Brabec 2009). All tests were computed using R statistical software, ver. 2.10.1 (R Development Core Team 2009).

Results

Sex ratio

Altogether, we sampled 190 newts (Table 1). The total sex ratio (M:F = 1.14:1) and the locality-

Table 1. Numbers of captured and stomach-flushed newts by locality, sex and month (individuals with empty stomachs in parentheses).

	April	May	June
Locality A: Male	16 (3)	15 (2)	16 (2)
Female	14 (1)	16 (5)	20 (1)
Locality B: Male	18 (7)	17 (2)	19 (2)
Female	3 (1)	14 (2)	22 (2)

specific sex ratio were unbiased (GLM: $\chi^2_1 = 0.76, p = 0.383$; and $\chi^2_1 = 1.76, p = 0.184$; respectively). The numbers of males and females did, however, vary differently during the reproduction period, and the interaction of sex and month was nearly significant ($\chi^2_2 = 5.72, p = 0.057$). While males were twice as numerous as females at the beginning of the breeding period (in April), the sex ratio was balanced during May and, in contrast to April, females slightly prevailed in June.

Overall diet composition and replete status of newts

A pooled sample of males and females from both localities contained 1417 identified prey items classified to 19 categories. The main prey categories consumed by newts were Cladocera at locality A and Isopoda at locality B (Table 2).

The number of newts with no prey in their stomachs (15.79% of total) significantly differed from the number of replete newts (chi-square test: $\chi^2_1 = 97.65, p < 0.001$). We found no differences in the numbers of replete and empty newts between localities (GLM replete and locality: $\chi^2_1 = 0.27, p = 0.600$) or between sexes ($\chi^2_1 = 0.68, p = 0.411$). More newts with empty stomach (30.77%) were found at the beginning of the breeding period (in April), while in June they comprised only 10%. However, the replete and month interaction was only nearly significant ($\chi^2_2 = 5.21, p = 0.073$), probably due to small numbers of newts.

Morphological characteristics and intersexual diet differences

SDIs of the population from localities A and B were 0.141 and 0.148, respectively. We revealed significant differences in SVL between sexes (GLM: $F_{1,155} = 263.07, p < 0.001$), localities ($F_{1,155} = 6.87, p < 0.01$), and among the months ($F_{2,155} = 8.47, p < 0.001$), but no interaction was found to be significant. Since month was significant and simultaneously consisted of three factor levels (April, May and June), we tested each factor level separately, and grouped the levels that did not differ. Male and female body sizes decreased from April to June. However, only

newts sampled in June were significantly smaller than the others (GLM *a-posteriori* comparison: $t = -3.97, p < 0.001$).

Regression analyses of the prey variables on SVL revealed different results for particular relationships. Whereas the numbers of prey categories and prey items were not affected by the body size of newts (linear regression: prey categories: $r^2 = 0.011, F_{1,158} = 2.80, p = 0.096$; prey items: $r^2 = 0.003, F_{1,158} = 0.53, p = 0.466$), the larger newts consumed significantly greater prey mass than did the smaller newts ($r^2 = 0.097, F_{1,158} = 18.17, p < 0.001$) (Fig. 1).

Despite separating the effect of different SVL between sexes, we found significant intersexual feeding differences. As compared with the males, the females consumed greater prey mass (GLMM: $\chi^2_1 = 67.17, p < 0.001$), as well as higher numbers of prey categories ($\chi^2_1 = 80.45, p < 0.001$) and prey items ($\chi^2_1 = 66.22, p < 0.001$). Because of non-significant interactions between variables with fixed (sex) and random (population) effects, we can conclude that consumption of prey by males and females did not differ between localities and over time (GLMM: prey mass: $\chi^2_2 = 0.01, p = 0.99$; number of prey categories: $\chi^2_2 = 1.78, p = 0.41$; number of prey items: $\chi^2_2 = 1.27, p = 0.53$).

Discussion

Overall diet composition

The dietary composition of the Alpine newt

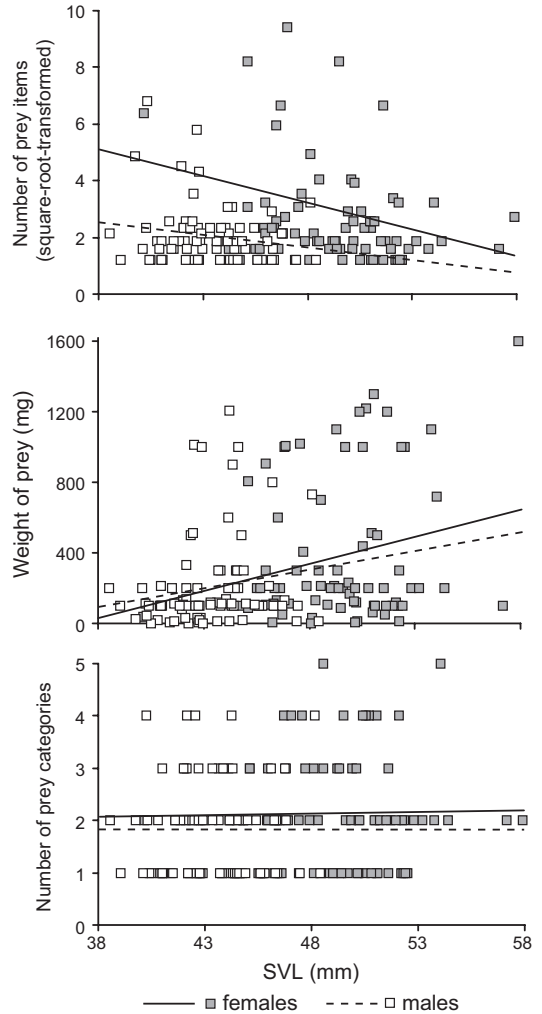


Fig. 1. Relationships in Alpine newts between snout-vent length (SVL) and prey variables.

Table 2. Main prey categories based on index of relative importance (%IRI) values. Only prey categories with %IRI > 1 are presented.

	Locality A		Locality B	
	Male	Female	Male	Female
Isopoda	2.04	0.50	88.55	96.04
Cladocera	49.27	61.39	3.89	2.64
<i>Rana</i> eggs	5.74	10.63	6.14	0.39
<i>Lumbricus</i>	6.40	15.47	0.02	0.31
Chironomidae larvae	16.52	1.80	0.30	0.02
Plecoptera larvae	12.63	2.47	0.12	0
Ephemeroptera larvae	1.02	5.63	0	0
Cyclopoida	1.68	0.03	0.41	0.27

shows that newts probably forage on a large variety of prey categories present in their environment. We did not estimate prey composition and density in the ponds, but adult newts are generally described as opportunistic feeders (Fasola & Canova 1992, Kutrup *et al.* 2005). Therefore, we hypothesized that newts (in the course of the breeding season) consumed prey which was dominant in the ponds or was easy to catch (Stephens & Krebs 1986).

Major prey categories (based on IRI%) were similar at both localities, but their importance differed. At locality B, newts consumed particularly Isopoda and *Rana* eggs (Table 2). These types of prey are foraged mainly in submerged vegetation or in shallow parts of a pond, respectively (Joly & Giacoma 1992, Denoël & Demars 2008). Newts at locality A, foraged on more diverse prey. This included Chironomidae and Plecoptera larvae, which were consumed especially by males, as well as *Rana* eggs and *Lumbricus*, which were consumed especially by females.

The occurrence of these diet categories and their importance for adult Alpine newts has been confirmed in previous works (Kminiak 1978, Rulík 1993, Denoël & Schabetsberger 2003). Cannibalism, most usual on eggs and sometimes on larvae (Miaud 1993, Rulík 1993, Denoël & Andreone 2003), was not found. Surprisingly, terrestrial invertebrates that had fallen onto the water's surface, sometimes considered an important source for the newt diet (Rulík 1993, Denoël *et al.* 2004), were weakly represented in our study.

Replete status of newts

The proportions of replete newts did not differ between localities and sexes. Since newts are ectotherms (Duellman & Trueb 1994), prey digestion, which theoretically takes three hours (Denoël & Demars 2008), is faster in a warmer environment, and is same for both sexes (Schabetsberger 1994). Nonetheless, we found more newts with empty stomachs in April (the beginning of the breeding period) than in June, which probably indicates low prey availability at this time. Maybe this is one of the reasons why females (Arntzen 2002) or males in poorer

condition (Kopecký & Šusta 2006) migrate to breeding sites later. Also, larvae hatching earlier in the season can suffer from low prey availability (Semlitsch 2008). A higher proportion of individuals with empty stomachs in April can also be a consequence of newts' sexual activity (Kminiak 1978). Because females' receptivity for mating decrease over the course of the breeding season (Gabor & Halliday 1997, Hoeck & Garner 2007), at it's the beginning, newts invest more time in mating than foraging.

Body size and diet differences

Difference in body length has been proposed as a mechanism of niche separation, which allows up to five newt species to coexist in a single water habitat (Arntzen & De Wijer 1989, Joly & Giacoma 1992). In such a case, the largest species capture the entire range of prey categories, whereas smaller newts are limited in their maximum prey size (Fasola & Canova 1992).

The same mechanism of niche isolation can also act at the intraspecific (intersexual) level. In sexually size-dimorphic species, the larger sex requires a higher absolute energy intake than does the smaller sex to meet metabolic requirements imposed by a larger body mass (Beck *et al.* 2007). This need can be met in several ways: the larger sex can consume (i) different or additional prey species, (ii) larger quantity of the same prey as the smaller sex, or (iii) heavier items from a particular prey category.

Our morphometric measurements confirmed that the Alpine newt is sexually dimorphic, with females larger than males (Griffiths 1996, Miaud *et al.* 2000). At both localities, SVL of females was about 15% greater than that of males. But this difference is probably not so strong as to allow females to forage on a separate and larger prey category that is inaccessible to males. For instance, earthworms (*Lumbricus*) were the largest prey items in our study, and they were found in the gut contents of both sexes. Thus, number of consumed prey categories was not affected by SVL of newts. Perhaps only due to their larger size, females are able to forage on larger prey items in particular prey categories. Such size-related predation has been found in newts by

Denoël and Joly (2001), Denoël and Andreone (2003) and Kutrup *et al.* (2005). We confirmed this indirectly, as SVL of newts had no influence on number of prey items consumed, and this relationship was even negative in both sexes. Only weight of prey was positively correlated with SVL (Fig. 1). We can, therefore, conclude that the assumption as to the preferences of larger newts for heavier prey rather than for capturing more numerous smaller items was correct (Joly & Giacoma 1992).

Intersexual diet differences

After separating the effect of SVL, we found that as compared with the males, the females consumed greater prey mass and higher numbers of both prey categories and prey items. It seems that the water part of the newt lifecycle is more challenging for females (e.g. egg laying requires more energy or diverse prey composition). Different requirements of females during this period comprise a source of intersexual differences not only in dimorphic but also in monomorphic species (Lewis *et al.* 2002). Although we did not measure changes in individual body condition during our study, consumption of more prey items, more diverse and heavier prey suggests that reproductive success in females is more sensitive to diet composition and total energy obtained during this period. This is consistent with an experimental observation of Bosca's newts (*Lissotriton boscai*), where females more than males used information about feeding of conspecifics, and also were more active during feeding when food was limited (Aragón 2009).

In the American rough-skinned newt (*Taricha granulosa*), sexual selection occurs more strongly in males, and in males it is more pronounced that higher number of matings leads to more offspring (Jones *et al.* 2002). We can assume that the same situation exists in Alpine newts, as during the reproductive season males are more colorful and have crests (Griffiths 1996). Males also often migrate to water earlier (Artnzen 2002), which can be very risky at some localities (Schabetsberger & Goldschmid 1994). Differences in quantitative characteristics (number of prey items, number of prey categories,

weight of prey) suggest that the males pay less attention than females to their own nutrition. Males probably invest more time in searching for mates, but there is no information on this subject for the studied species (Martin *et al.* 1989).

As pointed out by Fasola and Canova (1992), availability of prey is determined mainly by the conditions and composition of potential prey at a particular locality. Due to insignificant interaction between sex and population, we can conclude that males and females react to environmental factors affecting food in the same manner. For example, newts did not contain Cladocera in April and May, when the abundance of pelagic Cladocera greatly increased in June, both sexes reacted to this by increasing their consumption of this prey category at localities A (%IRI_{Cladocera}: males = 84.0, females = 85.6) and B (%IRI_{Cladocera}: males = 14.1, females = 9.0). Therefore, constraints in terms of prey availability affect both sexes identically.

To complete the overall picture of differences in the diet between sexes of newts, in future studies it will be very important to consider their terrestrial diet. Such studies are scarce for Caudata. One exceptional work was focused not on intersexual differences but on differences in the diet between unmetamorphosed and metamorphosed juveniles (Denoël 2004). Moreover, detailed knowledge about the energy content and composition of chemical elements in particular prey taxa could answer many questions that were beyond the scope of this study. Although on a scale of several months the two sexes exhibited similar reactions to prey availability, sex-mediated differences in prey consumption are probably environmentally determined (e.g. microhabitat selection, diel activity).

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