

## Terrestrial versus aquatic foraging in juvenile Alpine newts (*Triturus alpestris*)

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### Abstract

Many species of newts and salamanders forage in both terrestrial and aquatic environments during their life. However, the relative benefits of the two foraging patterns remain unknown because all previous studies have focused on only one habitat. The aim of this study was to find out which foraging tactic is the most successful in terms of energy intake. To this end, I analyzed trophic habits in metamorphosed juveniles in the Alpine newt, *Triturus alpestris veluchiensis*, inhabiting an alpine lake (Drakolimni) and the surrounding lands (Tymphi Mountains, northern Greece). The diet of the newts reflected the range of prey available in the two habitats, but aquatic newts also foraged on invertebrates that fell on the water surface. The two lifestyles have different energy outcomes. Terrestrial invertebrates provided high energy gains mainly to terrestrial juveniles because of the low number of this prey type in the lake. However, terrestrial juveniles are expected to suffer higher mortality (freezing on land is more probable than in deep waters) and a lower energy intake when air temperature is low, i.e., the main pattern in high-elevation sites, except during mid-summer. Persistence of the aquatic foraging tactics in the population may depend on a trade-off between costs and benefits.

### Résumé

De nombreuses espèces de tritons et de salamandres recherchent leur nourriture dans les environnements aquatiques et terrestres au cours de leur existence. Cependant, les bénéfices des deux tactiques restent inconnus car les précédentes études portaient sur un seul habitat. L'objectif de cette étude était de déterminer quelle tactique de recherche de nourriture avait le plus de succès en termes d'apport énergétique. A cette fin, j'ai analysé les habitudes trophiques chez des juvéniles métamorphosés du Triton alpestre *Triturus alpestris veluchiensis* habitant un lac alpin (Drakolimni) et les terres voisines (Monts Tymphi, nord de la Grèce). L'alimentation reflète la gamme de proies disponibles dans les deux habitats, mais les tritons aquatiques consommaient aussi des invertébrés terrestres tombés à l'eau. Les deux modes de vie ont des résultats énergétiques différents. Les invertébrés terrestres fournissent de hauts gains énergétiques principalement aux juvéniles terrestres étant donné la rareté de cette proie dans le lac. Cependant, les juvéniles terrestres sont supposés souffrir d'une plus haute mortalité (le gel sur terre est plus probable que dans l'eau) et d'une prise énergétique inférieure quand la température de l'air est basse, c'est-à-dire durant la majeure partie de l'année, le milieu de l'été excepté. La persistance des deux modes de recherches de nourriture dans la population dépend donc vraisemblablement d'un compromis entre différents coûts et bénéfices.

*Nomenclature:* Thorn & Raffaëlli, 2001.

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Foraging is a complex process of decisions that maximize the long-term average rate of energy intake of individuals able to choose specific prey types and hunt in particular patches (Schoener, 1971; Pyke, 1984; Stephens & Krebs, 1986). Foraging tactics depend on many factors, including the direct benefit from available resources, inter- and intraspecific exploitative competition, and aggression and predation (Huey & Pianka, 1981; Ziv et al., 1993; Lewis et al., 2001). Individuals are known to respond to resource depletion by exhibiting alternative tactics, such as resource partitioning (Schoe-

ner, 1974). This is particularly expected in taxa differing in morphological specializations under competitive pressure (Schluter, 1994) and exhibiting different activity periods (Ziv et al., 1993), habitat selection (Schlyter & Anderbrandt, 1993), and prey choice (Joly & Giacoma, 1992).

Most species with complex life cycles are expected to exhibit particular foraging patterns because they experience two different environments during their ontogeny. For example, some cnidarians shift from a benthic to pelagic habitat (Strathmann, 1993), some insects from a subterranean to an aerial mode

of life (Truman & Riddiford, 2002), and some amphibians from water to land (Wilbur, 1980). Habitat transition is usually obligatory for survival and reproduction. It is also important in allowing dispersal and taking advantage of transient resources (Wassersug, 1975; Wilbur, 1980). However, some species are facultative for such an environmental shift: while some individuals remain in their larval habitat after metamorphosis, others leave it. This is the case in some populations of amphibians, such as in the Alpine newt, *Triturus alpestris* (Denoël & Joly, 2001a; Denoël, 2003). After metamorphosis, juveniles usually leave the water and disperse on land until sexual maturation (Denoël & Joly, 2000; Miaud, Guyetant & Faber, 2000). Alternatively, they can continue foraging in the aquatic habitat (Denoël & Joly, 2001a). The existence of the two tactics within the same population offers an ideal opportunity to compare the advantages of remaining in the native habitat versus dispersing in a radically contrasting environment. It may also offer insights into the transition between complex life cycles and simple life cycles in species able to exhibit alternative developmental pathways (Whiteman, 1994; Denoël et al., 2002).

Foraging in aquatic habitats has been studied from several angles in newts and salamanders: feeding habits (Chacornac & Joly, 1985; Schabetsberger & Jersabek, 1995), resource partitioning between syntopic species (Griffiths, 1986; Joly & Giacoma, 1992) and alternative heterochronic morphs (Denoël & Joly, 2001a; Denoël & Schabetsberger, 2003; Denoël, Schabetsberger & Joly, 2004), and optimal use of aquatic patches (Whiteman et al., 1996). Differences in foraging tactics and performance by different morphs have also been demonstrated in laboratory experiments (Whiteman, Wissinger & Brown, 1996; Denoël, 2004b). Feeding habits in the terrestrial environment have been analysed in terrestrial species (Maglia, 1996; Anderson & Mathis, 1999), but remain poorly known in species exhibiting complex life cycles (only one study: Kuzmin, 1990) because of the cryptic terrestrial habits of these animals during this phase (Breuil, 1992; Griffiths, 1996).

The aim of this study was to compare the outcome of two different foraging patterns in the Alpine newt. To this end, I analyzed feeding habits and energetic gains of metamorphosed juveniles that remained in an alpine lake with those of metamorphosed juveniles that left the lake to inhabit the terrestrial environment.

## Methods

The study site, Drakolimni Lake, is located in the Tymphi Mountains, in Ioannina district, Epirus, north-west Greece (39° 59' N, 20° 47' E, 2,000 m elevation a.s.l.). Maximum diameter, volume, and maximum depth are 100 m, 16,000 m<sup>3</sup>, and 4.95 m, respectively. Vegetation is abundant near the shoreline. The lake is devoid of fish and is inhabited by a population of the Greek Alpine newt, *Triturus alpestris veluchiensis*, composed of larvae, juveniles, and adults (paedomorphs and metamorphs) (Denoël & Schabetsberger, 2003; Denoël, 2004a). The lake is surrounded by alpine pastures and rocks where only terrestrial juveniles have been observed. No predators were seen during day and night surveys in the terrestrial environment. This system has the benefit of allowing direct comparisons of individuals from the same population.

The study took place between 29 July and 3 August 1999. Forty-four aquatic metamorphosed juve-

niles were caught by dip-netting in the shoreline area of the lake and thirty-nine terrestrial metamorphosed juveniles were caught by hand on the ground near the lake (2–25 m from the shoreline). Despite intense day and night searching, no movements were seen across the two habitats during the study period.

Metamorphosed juveniles do not possess open gill slits and external gills and, unlike adults, do not have a swollen cloaca. All juveniles were measured from the tip of the snout to the extremity of the cloaca (snout–vent length) to the nearest 1 mm. Snout–vent lengths of the aquatic (mean  $\pm$  SE = 36.4  $\pm$  0.6 mm) and terrestrial (36.6  $\pm$  0.6 mm) individuals used in the present study did not significantly differ ( $t_{81} = 0.278$ ,  $P = 0.78$ ), enabling direct comparisons of food intake between the two habitats.

Immediately after capture, the newts were anaesthetized (0.5% phenoxyethanol solution) and their stomach contents were extracted using a stomach flushing technique described by Joly (1987). A catheter was inserted into the oesophagus and water was injected into the stomach, thereby expelling the prey items. Stomach contents were individually stored in vials and preserved in

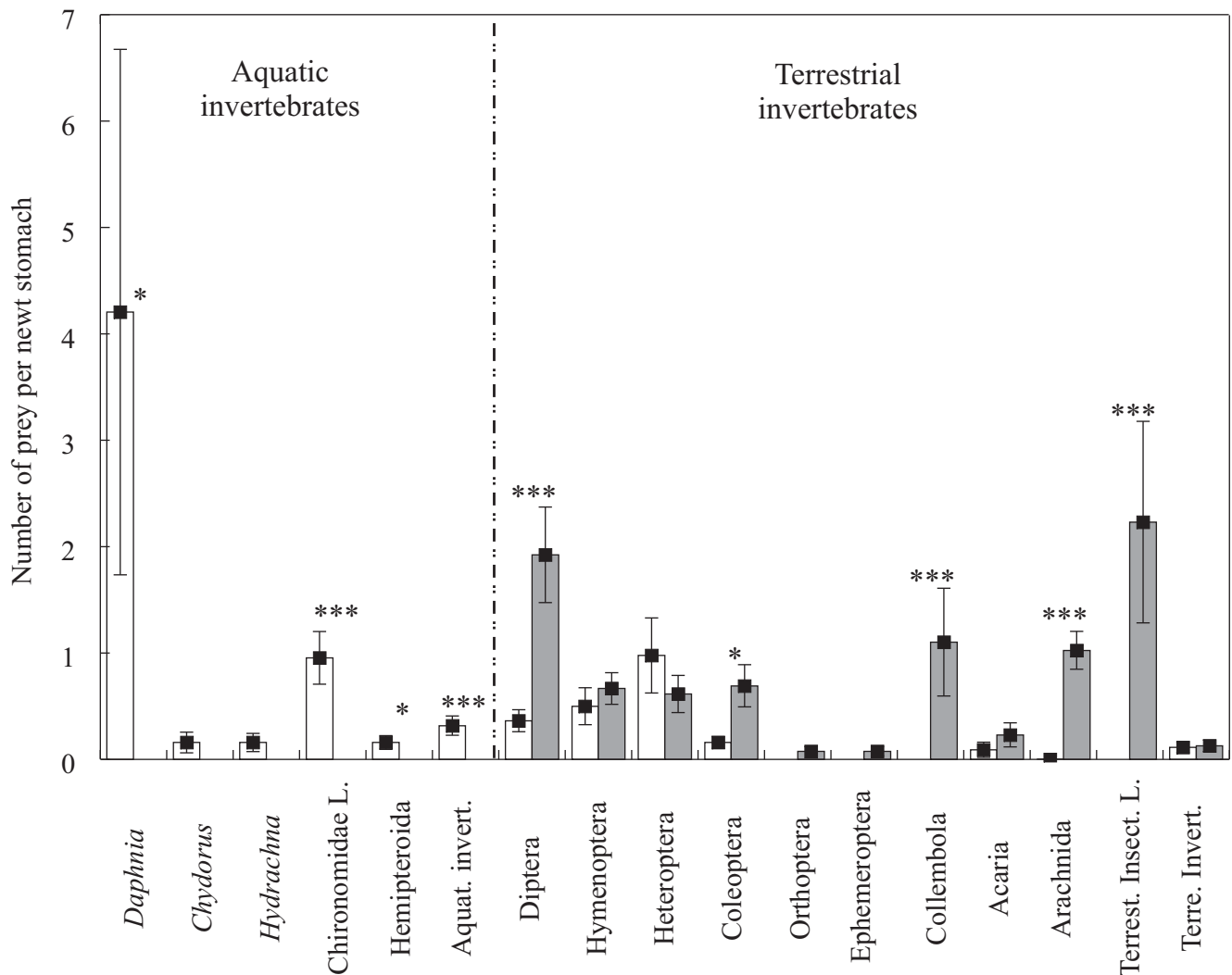
4% formaldehyde. Prey items were measured to the nearest mm along their longest axis and identified using a stereoscopic microscope. Their energy content was then estimated using specific relationships between size and energy contents (Cummins & Wuickelck, 1971; Jorgensen, 1979). Newts were kept in containers until the end of the whole sampling period to avoid recapture. They were released at their place of first capture on August 3rd, 1999.

A multivariate analysis of variance (MANOVA) was used to treat the number of items of each prey type as a different dependent variable, whereas univariate analyses (ANOVA) were done on each prey type separately. Student *t*-tests were computed to compare the energy content of the prey in the stomachs of aquatic and terrestrial juveniles. To determine the significance of the difference between the energy content of aquatic and terrestrial invertebrates caught by aquatic juveniles, a paired *t*-test was used. Data were log or squareroot (+ 0.1) transformed to fit the conditions of ANOVAs (Sokal & Rohlf, 1995), but to improve readability presented values are not transformed.

## Results

There was a significant difference in the diet of terrestrial and aquatic juveniles (MANOVA:  $\lambda = 0.304$ ,  $F_{17,65} = 8.777$ ,  $P < 0.001$ ). Terrestrial juveniles consumed only terrestrial prey from a wide variety of taxa: mainly insect larvae, adult Diptera, Hymenoptera, Heteroptera, Coleoptera, Collembola, and Arachnida, but also Orthoptera, Ephemeroptera, and Acari (Figure 1). Aquatic juveniles preyed on both aquatic and terrestrial invertebrates present in the water. They ate mainly *Daphnia* and larval Chironomidae, but also Chydoridae, Hydracarina, and Hemipteroida. They also consumed Diptera, Hymenoptera, Heteroptera, and, more rarely, some Coleoptera and Acari (Figure 1).

Terrestrial juveniles had a significantly higher number of Diptera ( $F_{1,81} = 14.932$ ,  $P < 0.001$ ), Coleoptera ( $F_{1,81} = 6.666$ ,  $P < 0.05$ ), Collembola ( $F_{1,81} = 13.456$ ,  $P < 0.001$ ), Arachnida ( $F_{1,81} = 54.260$ ,  $P < 0.001$ ), and insect larvae ( $F_{1,81} = 19.860$ ,  $P < 0.001$ ), but a significantly lower number of *Daphnia* ( $F_{1,81} = 6.257$ ,  $P < 0.05$ ), larval Chironomidae ( $F_{1,81} =$



**Figure 1.** Stomach contents of metamorphosed Alpine newt juveniles (*Triturus alpestris*): number of prey in aquatic (open bars) and terrestrial (shaded bars) individuals. Invert.: invertebrates; L: larvae. Data are means  $\pm$  1 SE. \*  $P < 0.05$ , \*\*\*  $P < 0.001$  (MANOVA).

24.444,  $P < 0.001$ ), and Hemipteroida ( $F_{1,81} = 5.777$ ,  $P < 0.05$ ) in their stomachs than the aquatic juveniles (Figure 1).

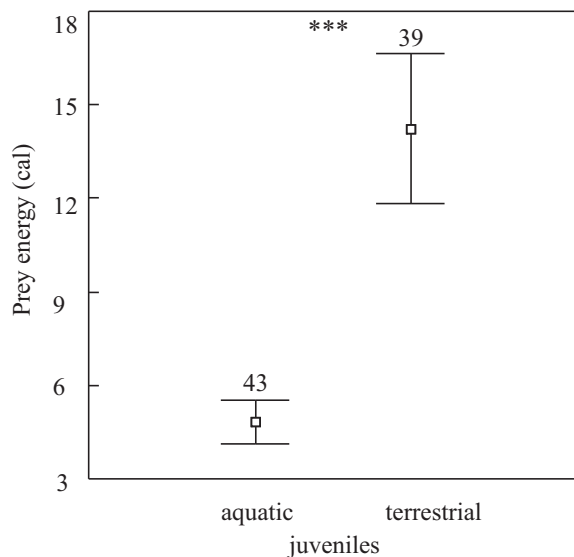
Both terrestrial and aquatic juveniles foraged on prey of different length (between ca 1 and 11 mm). There were no significant differences between the mean size of the prey caught by terrestrial (mean  $\pm$  SE =  $2.74 \pm 0.14$  mm) and aquatic ( $2.68 \pm 0.26$  mm) juveniles ( $t_{78} = 1.275$ ,  $P = 0.21$ ). Although not significant in aquatic juveniles ( $F_{1,40} = 0.019$ ,  $P = 0.89$ ), the regression of mean prey length on newt snout-vent length was significant in terrestrial juveniles ( $\log \text{SVL} = -3.786 + 1.317 \log \text{prey size}$ ;  $r = 0.39$ ,  $F_{1,36} = 6.442$ ,  $P < 0.05$ ).

The total energy content of the stomachs significantly differed in terrestrial (mean  $\pm$  SE =  $59.57 \pm 10.04$  J) and aquatic ( $20.14 \pm 2.93$  J) juveniles ( $t_{81} = 3.280$ ,  $P < 0.01$ ) (Figure 2). Sixty-two percent of the energy intake of aquatic juveniles came from aquatic prey ( $12.43 \pm 2.57$  J), and the other 38% came from terrestrial invertebrates caught in water ( $7.71 \pm 1.89$  J). This difference is significant (paired  $t_{43} = 2.057$ ,  $P < 0.05$ ). Predation on terrestrial invertebrates was significantly higher in the terrestrial environment ( $59.57 \pm 10.04$  J per stomach of terrestrial juvenile) than in the lake ( $7.71 \pm 1.89$  J per stomach of aquatic juvenile) ( $t_{81} = 3.400$ ,  $P < 0.001$ ).

## Discussion

Metamorphosed Alpine newts (*Triturus alpestris*) can exhibit a foraging strategy composed of two different feeding tactics. While a part of the population stays in water to forage, the other part lives on land and feeds only in this habitat. These two behavioural patterns have different consequences in terms of both diet composition and direct energetic benefits.

On land, juveniles foraged on the different available invertebrates, mainly dipterans, spiders, springtails, and insect larvae. In contrast, when in water, juveniles preyed on aquatic organisms, mainly daphnids and chironomid larvae. These results are not really surprising as they reflect the natural composition of prey taxa in the aquatic and terrestrial components. However, aquatic juveniles also foraged on terrestrial prey that fell on the water surface, a well known foraging tactic in this species (Chacornac & Joly, 1985; Denoël & Joly, 2001a), including in adults from the studied population (Denoël & Schabetsberger, 2003). This tactic allows newts to supplement their diet in oligotrophic waters in which the biomass of aquatic organisms is low (Chacornac & Joly, 1985). In Drakolimni lake, aquatic juveniles increased their energy intake by



**Figure 2.** Mean ( $\pm 1$  SE) energetic equivalent of stomach content of aquatic ( $n = 44$ ) and terrestrial ( $n = 39$ ) metamorphosed Alpine newt juveniles (*Triturus alpestris*). \*\*  $P < 0.01$  ( $t$ -test).

60% by using this additional exogenous resource (this study).

When individuals or species differ in size, it can be expected that they use different resources (Hutchinson, 1959). This trait cannot be the reason for different feeding tactics in aquatic and terrestrial juveniles, because they do not differ in body size. However, within each component, individuals may focus differently on some specific prey sizes according to their own size. Such a pattern has been observed in several amphibian species, including Alpine newts (Leff & Bachmann, 1986; Kuzmin, 1991; Denoël & Joly, 2001b; Denoël & Andreone, 2003). Such size-related predation was found in this study, but it was slight and only present in terrestrial juveniles.

Optimal foraging theory predicts that individuals will choose the most profitable patch in their environment. That means that animals should switch to a more profitable environment when foraging gets too costly in a patch that does not provide enough energy (Norberg, 1977; Pyke, 1984; Stephens & Krebs, 1986). Ontogenetic niche shift is believed to favour optimal growth by taking advantage of better resources (Wassersug, 1975; Arendt & Wilson, 1997). Because growth rates are higher in larvae and juveniles than in adult urodeles (Miaud, 1996; Miaud, Guyétant & Faber, 2000) and because size is correlated with fecundity (Semlitsch, 1985), sub-adult stages are particularly expected to exhibit an optimal choice of resource use.

In this study, after metamorphosis from aquatic larvae, juveniles had the potential of feeding in either the terrestrial or the aquatic environment. These two foraging tactics had different immediate benefits. Juveniles that chose to leave water for land got a higher energy intake from their food than juveniles that stayed in water. Although aquatic juveniles obtained energy by foraging on terrestrial taxa, the low number of these exogenous prey in their diet was a disadvantage in comparison with terrestrial individuals. These results seem to indicate that the persistence of an aquatic mode of life in juveniles is not optimal, suggesting that juveniles should shift habitat to get more nutritional energy. However, there are several reasons that may explain the persistence of the apparently non-optimal foraging tactic in the studied population.

First, the foraging pattern is strongly connected with the local meteorological conditions. Because newts are ectotherms, their terrestrial activity closely depends on temperature and humidity (Rome et al., 1992; von Lindeiner, 1992). The study took place during summer, i.e., in favourable conditions for terrestrial foraging. Outside the summer period, newt activity on land is considerably reduced, with newts remaining in their shelters during long periods (Pinder, Storrey & Ultsch, 1992). Metabolism is also considerably lowered at low temperatures (Schabetsberger, 1994). In water, however, newts can stay active even if the water surface freezes (M. Denoël, pers. observ.). Newts can thus take advantage of aquatic foraging for a longer period of time than terrestrial juveniles (at least twice as long). Total energy intake per year remains to be determined, however. In addition, aquatic newts may compensate for the lower quality food by feeding more frequently and having a higher gut turnover (Schabetsberger, 1994). Only capture-mark-recapture studies can collect accurate data on variations in individual activity, habitat use, and feeding, but such studies would be difficult in this case because newts usually have a secretive terrestrial phase (Joly & Miaud, 1989; Breuil, 1992). Secondly, mortality rates are different on land compared to water because the lake does not freeze completely and is not anoxic during winter (cf. the presence of overwintering branchiate individuals: Denoël & Schabetsberger, 2003; Denoël, 2004a). On land, juveniles are at the risk of not finding safe shelters during cold nights, particularly during winter (Pinder, Storrey & Ultsch, 1992).

In conclusion, both aquatic and terrestrial life are viable options for metamorphosed juveniles. Although aquatic foraging provides a lower immediate energy benefit, the persistence of the two patterns may result from a trade-off between different short- and long-term benefits (Denoël et al., 2002). Environmental conditions, resource availability, competition, mortality rates, pedomorphosis, and dispersion are all factors that remain to be determined to fully understand the dynamics of populations occupying both aquatic and terrestrial habitats after metamorphosis. However, this study shows that terrestrial feeding at high-elevation environments is a successful tactic and that, in these systems, newts can get higher benefits from land than from water.

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