

The benefits of heterospecific oophagy in a top predator

Mathieu Denoël* & Bertrand Demars

Abstract

Oophagy is a behavioural pattern that has been found in a large variety of predator species in the animal kingdom. In contrast to other modes of feeding, it is peculiar in that it involves the detection, capture and ingestion of immobile prey. Several hypotheses have been proposed to explain the evolutionary origin and persistence of this pattern, but they have rarely been tested. The aim of this study was to compare the benefits of a heterospecific oophagous tactic over a non-oophagous diet in terms of biomass intake. To this end, stomach contents were gathered by flushing the stomachs of male and female Alpine newts (*Mesotriton alpestris*) found in forestry ruts (i.e. pools caused by traffic) during their reproductive period. Prey items were identified, classified into functional categories and their dry mass determined. Frog (*Rana temporaria*) eggs are valuable prey items that give a higher biomass intake to individuals foraging on them than on those relying on invertebrates. Both sexes of newts practice oophagy but frog eggs are a transient resource that is only available during a part of their aquatic phase. Consequently, the newts adjust their diet to invertebrate predation later in the season after the peak of the frogs' breeding season. Oophagy is thus facultative and not obligate in the study species. The correlated occurrence of prey and predator, similarities between frog eggs and mobile potential prey (tadpoles), and high resource intake are all in favour of the occurrence and persistence of an oophagous feeding tactic.

© 2008 Elsevier Masson SAS. All rights reserved.

Keywords: Biomass intake; Feeding tactic; Oophagy; Optimal foraging; Resource use

Introduction

Oophagy is a widespread feeding behaviour in the animal kingdom, with examples in a variety of organisms, such as molluscs (Järnegen et al., 2005), insects (Kudo and Nakahira, 2004), fish (Ochi et al., 1999), amphibians (Denoël and Andreone, 2003), reptiles (de Queiroz and Rodriguez-Robles, 2006), birds (Burger, 1980), and mammals (Estrada et al., 2002). Because eggs are immobile animal products, they imply behavioural specificities in the predators (de Queiroz and Rodriguez-Robles, 2006) but also morphological adaptations because of their size and structure (Coleman et al., 1993, Herrel et al., 1997 and Scanlon and Shine, 1988). Obligate oophagy occurs when predators are solely dependent on eggs (Järnegen et al., 2005) whereas facultative oophagy is a more flexible pattern that allows a shift of diet according to egg availability (Dayton and Fitzgerald, 2005 and Ochi et al., 1999). Oophagy can be directed towards conspecific or heterospecific prey (Hoff et al., 1999). Whereas the former is a kind of cannibalism (Miaud, 1993), and sometimes associated with the production of trophic eggs to feed young (Brust, 1993 and Kudo and Nakahira, 2004), the evolution of heterospecific oophagy is less well understood (de Queiroz and Rodriguez-Robles, 2006 and Järnegen et al., 2005).

Different hypotheses have been proposed to explain the origin and ultimate mechanisms of oophagous behaviour. Species that already feed on other life stages of the egg-producing prey species may be particularly likely to feed on their eggs if the eggs are laid in the area where the predator normally feeds and if the eggs share some traits with the adult animals (de Queiroz and Rodriguez-Robles, 2006). From an adaptive perspective, eggs can provide a high biomass intake which may supply an important source of sustenance during egg laying, mating and emigration (Kaplan and Sherman, 1980). More indirectly, predators could protect themselves from future competition or predation from the prey species by eliminating its eggs (Kaplan and Sherman, 1980).

In amphibians, feeding has been extensively studied with particular emphasis on aquatic behaviour (Duellman and Trueb, 1994 and Griffiths, 1996). Caudates are generally adapted for predation on a large variety of mobile prey (Deban and Wake, 2000) and can exhibit varied morphological and behavioural specializations related to feeding (Denoël, 2004, Denoël and Joly, 2001 and Denoël et al., 2007). The cannibalistic ingestion of eggs and larvae has often been reported (Denoël and Andreone, 2003, Denoël and Schabetsberger, 2003, Denoël et al., 2006 and Miaud, 1993). Caudates coexist with other species,

Laboratory of Fish and Amphibian Ethology, Behavioural Biology Unit, Department of Environmental Sciences, University of Liège, 22 Quai van Beneden, 4020 Liège, Belgium

*Corresponding author. Fax: +32 4 366 5113. E-mail address: mathieu.denoel [a] ulg.ac.be (M. Denoël).

including anurans that also live in water for part of their life cycle. When coexisting species lay eggs in a shared habitat, heterospecific oophagy is likely to occur (Cooke, 1974, Griffiths and Mylotte, 1987, Stoch and Dolce, 1984 and Walters, 1975). This pattern has also been found in the Alpine newt (Kuzmin, 1990, Kwet, 1996, Rulik, 1993 and Sattmann, 1989). Despite this, heterospecific oophagy remains poorly understood with few studies targeting this tactic, specifically its biomass input. Such considerations are pre-requisites for understanding the value of these feeding specializations on transient resources.

The aim of this study was to determine the benefits of heterospecific oophagy in order to better understand the behavioural ecology and evolution of this feeding specialization. To this end, we determined the diet and biomass intake of Alpine newts in six aquatic habitats during two sampling periods. Our hypothesis is that heterospecific oophagy is providing a higher input to individuals which exhibit this behavioural pattern.

Methods

The study area is located in Matagne-la-Petite wood, South of Namur, in Belgium (4°38'48" E, 50°7'7" N) at an elevation ranging from 180 to 210 m a.s.l. The wood is composed of both deciduous and coniferous trees and includes a large number of large paths on which traffic is not allowed except with special permits. Most unpaved paths contain ruts (i.e., holes) caused by the occasional vehicular traffic. These holes can be filled up by water and then utilized by amphibians for breeding.

The predator studied was the Alpine newt *Mesotriton alpestris alpestris* (Laurenti, 1768) (previously known as *Triturus a. alpestris*). This is a species which occupies both aquatic and terrestrial habitats during its adult life (Denoël, 2003). In the study population, adults migrate after the cold winter period (e.g., March) to a water body in which they reproduce and feed. They usually remain within the water for a few weeks or months but a few adult individuals were still present in the water in May (Denoël, 2007; M. Denoël and B. Demars, personal observation).

Rana temporaria temporaria Linnaeus, 1758 served as the model target of heterospecific oophagy by newts. Although these frogs often remain in aquatic habitats for long periods, they were transients in the temporary habitats where our study took place.

Table 1. Number of stomach-flushed Alpine newts in the forestry ruts (i.e. pools caused by vehicular traffic) and proportion of newts foraging on common frog eggs

Rut (pool)	March		April	
	<i>n</i> (♂-♀)	Egg pre- dators	<i>n</i> (♂-♀)	Egg pre- dators
A13	21 (15-6)	61%	18 (11-7)	11%
A15	27 (15-12)	0%	20 (12-8)	5%
C05	25 (21-4)	4%	4 (3-1)	25%
H06	13 (7-6)	0%	4 (1-3)	0%
H28	10 (6-4)	0%	10 (7-3)	10%
T01	33 (29-4)	58%	23 (14-9)	4%

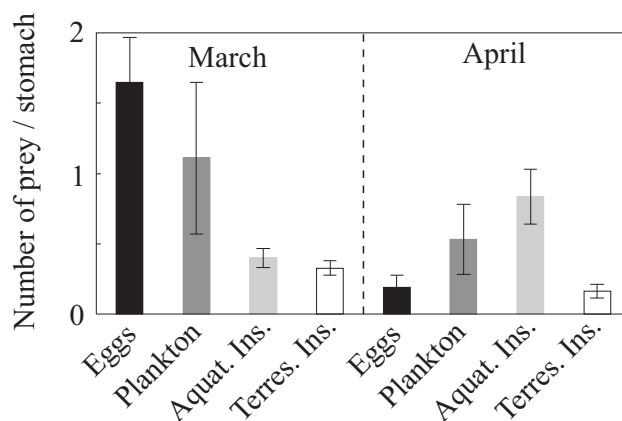


Fig. 1. Mean number of prey (\pm SE) per stomach in Alpine newts in March ($n = 129$) and April ($n = 78$).

The peak of their reproductive period in the study site was during March but some late breeders laid eggs in April (M. Denoël and B. Demars, personal observation).

We sampled adult newts by dip netting in six ruts (i.e., pools) which contained a sufficient number of adult individuals (Table 1). Sampling took place in March ($n = 133$) and April 2004 ($n = 79$). Newts were kept in refrigerated boxes (about 5 °C) and stomach-flushed within 3 h to avoid prey digestion (Joly, 1987 and Schabetsberger, 1994). Newts were released the same day into their natural habitat. Stomach contents were stocked in separate vials. Prey was determined using a stereomicroscope. Prey items were measured (total length) and classified into four functional categories: frog eggs (*Rana temporaria*), plankton, aquatic insects (including aquatic larvae of terrestrial insects), and terrestrial invertebrates that had fallen on the water surface. Dry weight of stomach contents was obtained by using regression equations of the dry weight on size for each kind of prey.

A multivariate analysis of variance was used to test for the effect of sex, pond and month on diet and dry mass. The Bonferroni post-hoc test was used to take into account the experiment-wise error rate. All values were transformed appropriately before analysis to reach normality (square root + 0.5 for counts, log10 for continuous data) (Sokal and Rohlf, 1995 and Statsoft-France, 2005).

Results

3.1. Feeding habits

Newts foraged on the four functional prey categories, including eggs, both in March and April (Fig. 1). The diet differed between the two study months (Wilk's $\lambda = 0.887$, $F_{4,202} = 6.457$, $P < 0.001$), with more eggs ($F_{1,205} = 15.177$, $P < 0.001$) and terrestrial insects ($F_{1,205} = 4.583$, $P < 0.05$) but fewer aquatic insects ($F_{1,205} = 5.193$, $P < 0.05$) eaten in March than in April. In March, newts foraged significantly more on eggs than on the other prey categories (Bonferroni post-hoc test, vs. plankton: $P < 0.05$, vs. aquatic insects: $P < 0.01$, vs. terrestrial insects: $P < 0.01$). In April, newts consumed fewer eggs than aquatic insects ($P < 0.01$). In March, 27% of newts consumed eggs while in April only 10% consumed eggs.

Both males and females foraged on the same functional categories. They differed significantly in

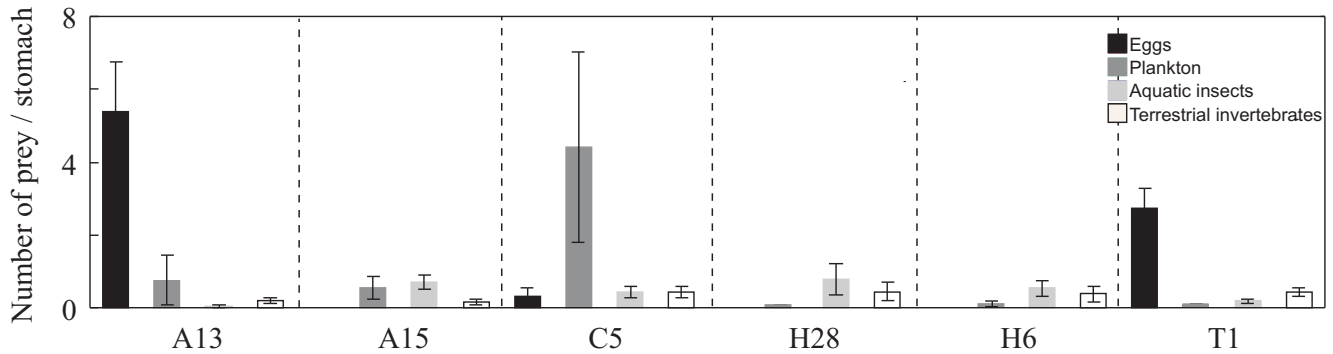


Fig. 2. Mean number of prey (\pm SE) per stomach in Alpine newts in different ruts (i.e. pools) in March ($n = 129$).

their diets in April (Wilk's $\lambda = 0.789$, $F_{4,74} = 4.957$, $P < 0.01$) but not in March (Wilk's $\lambda = 0.942$, $F_{4,123} = 1.904$, $P = 0.11$). In April, the females ingested more terrestrial invertebrates than males ($F = 16.543$, $P < 0.001$) but no significant differences were found for the other prey categories.

The diet differed between pools in March (Wilk's $\lambda = 0.505$, $F_{20,402} = 4.601$, $P < 0.001$) but not in April (Wilk's $\lambda = 0.674$, $F_{20,402} = 1.473$, $P = 0.09$). In March, the highest abundance of eggs per stomach was found in the pools A13 and T01 (Bonferroni post-hoc test, all $P < 0.05$) (Fig. 2).

Because there were not enough egg-eating newts to allow diet analysis per pool, we selected the two most inhabited pools: A13 and T01 for this analysis. In these two pools, the diet (excluding eggs) of newts which consumed eggs was not significantly different from that of newts which did not consume eggs (A13: Wilk's $\lambda = 0.798$, $F_{3,17} = 1.432$, $P = 0.27$; T01: Wilk's $\lambda = 0.863$, $F_{2,30} = 2.372$, $P = 0.11$) (Fig. 3).

3.2. Prey biomass

The ingested dry biomass of each prey category differed between the two study months (Wilk's $\lambda = 0.918$, $F_{4,202} = 4.520$, $P < 0.01$), but the difference was only due to the predation on eggs which produced a higher biomass intake in March than in April ($F_{1,205} = 14.623$, $P < 0.001$) (Fig. 4). In March, eggs represented a higher biomass intake than plankton and terrestrial insects (Bonferroni, $P < 0.001$), but in April the eggs represented a lower biomass intake than the aquatic insects (Bonferroni, $P < 0.001$).

The egg-eating newts had a significantly higher biomass intake than those not eating eggs ($t_{205} = 9.211$, $P < 0.001$) (Fig. 5). This effect remained after removing newts with empty stomachs from the analysis (4.58 ± 0.57 mg vs. 12.08 ± 1.49 , $t_{156} = 6.976$, $P < 0.001$). The effect is also significant in looking separately in the pools where such predation was found in March (A13: $t_{19} = 6.244$, $P < 0.001$, T01: $t_{31} = 4.255$, $P < 0.001$) (Fig. 5).

Discussion

Our results show that heterospecific oophagy is a common and efficient tactic in the study population because (1) it is a frequent pattern, (2) it constitutes an additional resource in small temporary habitats, and (3) it provides a higher biomass intake than predation on other prey categories.

Despite opportunistic feeding, the ingestion of some prey items can be particularly advantageous for predators if they minimize their energy:time

ratio (Bell, 1991 and Stephens and Krebs, 1986). Specialization on heterospecific eggs can therefore be an adaptive trait. For instance, cannibal morphs obtain benefits in consuming large heterospecific prey and conspecific larvae (Whiteman et al., 2003), paedomorphic newts are highly efficient at sucking large planktonic organisms (Denoël, 2004), and metamorphic newts ingest voluminous terrestrial prey that fall on the water surface (Chacornac and Joly, 1985 and Denoël and Joly, 2001). The direct benefits of oophagy have been little documented but Brust (1993) showed that the more unfertilized trophic eggs an obligatorily oophagous *Dendrobates pumilio* tadpole received, the faster it grew. In this study, heterospecific oophagy was shown to be particularly beneficial to newts because eggs are a reliable prey organism that cannot escape. *Rana temporaria* eggs are available in large quantities (clutches contain around 1000 eggs on average, i.e. around 12 g of wet weight: Gibbons and McCarthy, 1986), and provide a high biomass. In comparison with newts

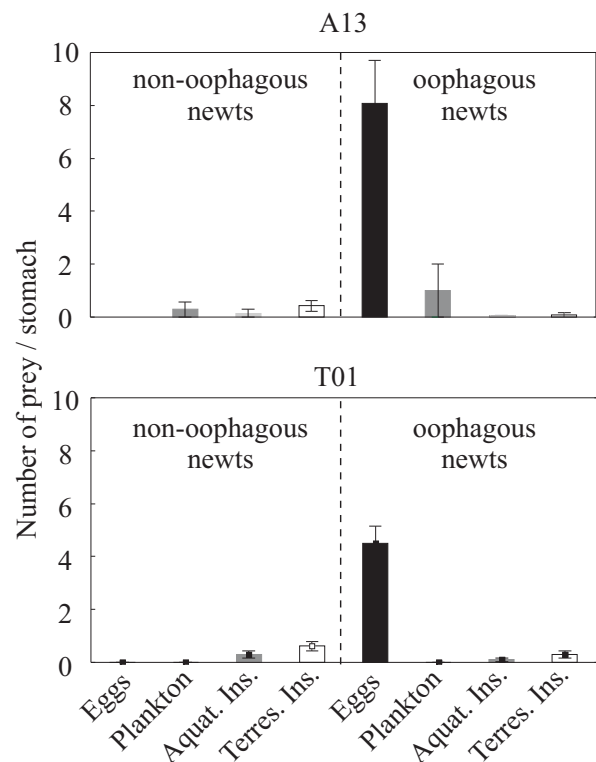


Fig. 3. Mean number of prey (\pm SE) per stomach in syntopic non-oophagous and oophagous Alpine newts in March (A13: $n = 21$, T01: $n = 33$).

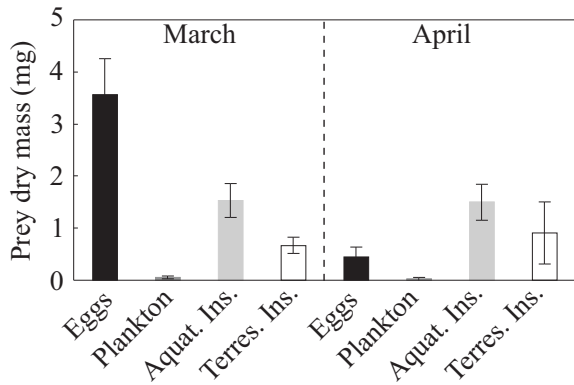


Fig. 4. Mean biomass of prey (\pm SE) per stomach in Alpine newts in March ($n = 129$) and April ($n = 78$).

that did not consume eggs, oophagous individuals had stomach contents more than twice as heavy. As our measurements were obtained on dry mass, these differences were not due to variations in water content. Moreover, frog eggs are devoid of inedible structures (e.g., cuticle), which could lower energy intake, making them an even more profitable prey item. It has been shown that the non-polar lipid content (i.e., the major source of energy) of eggs is proportional to their dry mass (Komoroski and Congdon, 2001 and Komoroski et al., 1998). This high biomass intake could have long-term advantages because urodeles need to boost their reserves to survive winter and increase their fitness for the following reproductive season (Denoël et al., 2002 and Semlitsch, 1985). The biomass acquisition hypothesis as the basis for oophagy (Kaplan and Sherman, 1980) is thus largely supported.

Although competition has been proposed as an ultimate factor promoting oophagy, direct competition between newts and tadpoles remains to be established. These organisms usually forage on different prey items (Harrison, 1987 and Loman, 2001; this study) but in some cases tadpoles can cannibalize conspecifics, including *Rana temporaria* (M. Denoël and M. Bichot, personal observation). Indirect competition cannot be excluded because tadpoles may reduce the mass of plankton and other invertebrates through consuming the phytoplankton. Adult frogs share some dietary habits with newts in foraging on terrestrial invertebrates, but are probably not direct competitors because they do not seem to forage in water (Blackith and Speight, 1974, Houston, 1973 and Loman, 1979).

Frog eggs are not laid continuously during the aquatic phase of adult newts (Denoël, 2007; perso-

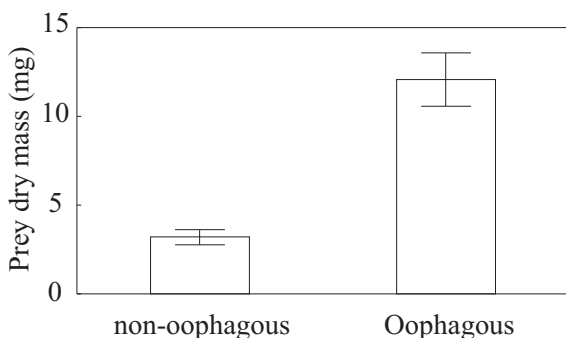


Fig. 5. Mean biomass of stomach contents (\pm SE) in non-oophagous and oophagous Alpine newts ($n = 207$).

nal observation), so this is a transient resource on which newts focus when it is available. The higher number of egg-eating newts in March rather than in April reflects the peak of the reproductive period of common frogs in the study area in March (personal observation). Such temporary specialization can be seen as an alternative tactic in newts (*sensu* Gross, 1996), which take advantage of passing opportunities (Dunbar, 1982). Specialized foraging on large prey, described above, is also a temporary pattern. When the weather deteriorates and terrestrial insects become less available, newts start to focus primarily on aquatic prey (Denoël and Joly, 2001); cannibal salamander larvae are not always cannibalistic and can become planktonivorous (Denoël et al., 2006) whereas adults can breed in permanent waters but move to temporary aquatic habitats in which large branchiopod crustaceans are abundant (Denoël et al., 2007).

Differences between the sexes have often been found in the selection of prey. This may be explained by different habitat use, morphology and strategy (Joly and Giacoma, 1992). For instance, in newts, conspecific oophagy was more frequent in females than in males (Denoël and Andreone, 2003 and Miaud, 1993). However, despite the larger size of females (Denoël, 2007), no significant variation was found in terms of heterospecific oophagy in the present study but was, nevertheless, observed in terms of their predation on terrestrial invertebrates where there was a higher rate of capture in females than in males. No conspecific oophagy was observed in the study population.

The two proximate mechanisms proposed by de Queiroz and Rodriguez-Robles (2006) are likely to occur, but with some specificities. Because Alpine newts can detect prey on the basis of chemoreception (Joly, 1981), similarities at this level between eggs and tadpoles could have favoured the evolution of the diet towards egg-eating behaviour. This mechanism is likely because newts often forage on mobile prey which is detected by vision and possibly mechanoreception (Martin, 1982). Although no tadpoles were found in the diet of the newts in this study, predation on tadpoles has been found in other newt populations (Griffiths and Mylotte, 1987) and in laboratory experiments (Heusser, 1971, Reading, 1990, Walters, 1975 and Zahn, 1997). In contrast to other groups such as snakes (de Queiroz and Rodriguez-Robles, 2006), specific feeding predispositions are not directed to the animals that lay the eggs because Alpine newts are not able to ingest frogs. The hypothesis of feeding predispositions (de Queiroz and Rodriguez-Robles, 2006) can thus be extended to the ingestion of larvae. The fact that tadpoles live in the same habitat in which eggs are laid should increase the probability of predation. On the other hand, the hypothesis that egg-eating came before the evolution towards tadpole predation cannot be rejected at this stage. Because newts can forage on their own eggs (e.g. Denoël and Andreone, 2003), although not observed in the study population, foraging on frog eggs may have originated from cannibalism and would have alleviated the cost of ingesting related conspecifics (Pfennig and Collins, 1993).

Despite the widespread occurrence of heterospecific oophagy in the animal kingdom, this remains a topic that has not been well studied, apart from a mention in a study of predator diets (de Queiroz and Rodriguez-Robles, 2006). The present study is therefore novel in presenting the benefits of this mode of feeding in terms of biomass intake. The next step would be to undertake more long-term observational studies and to test the derived hypotheses with

experimental work. In particular, the fitness (i.e. fecundity or mating success) of egg-eating versus invertebrate-eating newts should be compared. Large food-web analyses are particularly recommended because of the ecological impact of a recruitment drop in prey populations (Banks and Beebe, 1987). This was not the aim of this study but our results strongly suggest that a high rate of egg feeding could affect the structure of prey populations and other dependent organisms as common frogs often lay their eggs in the same habitat as newts.

Acknowledgments

We are grateful to R.A. Grant, A. de Queiroz and L.R.G. Raw for their constructive comments on the manuscript, Ph. Lebrun and J.P. Thomé for providing access to their laboratories, C. Joaquim-Justo and M. Louvet for their help in the laboratory, Ministère de la Région Wallonne for authorizing this study, Cantonnement de Viroinval for allowing access to the study site, and Ministère de l'Équipement et des Transports for logistic support. M.D. is a Research Associate at the Fonds de la Recherche Scientifique (FNRS, Belgium). This study was supported by FRS-FNRS grant number 1.5.199.07.

References

- Banks B., Beebe, T.J.C., 1987. Spawn predation and larval growth inhibition as mechanisms for niche separation in anurans. *Oecologia* 72, 569-573.
- Bell W.J., 1991. Searching behaviour. The behavioural ecology of finding resources. Chapman & Hall, London.
- Blackith R.M., Speight, M.C.D., 1974. Food and feeding habits of the frog *Rana temporaria* in boglands habitats in the West of Ireland. *J. Zool.* 172, 67-79.
- Brust D.G., 1993. Maternal brood care by *Dendrobates pumilio*: a frog that feeds its young. *J. Herpetol.* 27, 96-98.
- Burger J., 1980. Territory size differences in relation to reproductive stage and type of intruder in herring gulls (*Larus argentatus*). *Auk* 97, 733-741.
- Chacornac J.M., Joly, P., 1985. Activité prédatrice du triton alpestre (*Triturus alpestris*) dans un lac alpin (2125 m, Alpes françaises). *Acta oecol.* 6, 93-103.
- Coleman K., Rothfuss, L.A., Ota, H., Kardong, K.V., 1993. Kinematics of egg-eating by the specialized Taiwan snake *Oligodon formosanus* (Colubridae). *J. Herpetol.* 27, 320-327.
- Cooke A.S., 1974. Differential predation by newts on anuran tadpoles. *Brit. J. Herp.* 5, 386-390.
- Dayton G.H., Fitzgerald, L.A., 2005. Priority effects and desert anuran communities. *Can. J. Zool.* 83, 1112-1116.
- de Queiroz A., Rodriguez-Robles, J.A., 2006. Historical contingency and animal diets: The origin of egg eating in snakes. *Am. Nat.* 167, 682-692.
- Deban S.M., Wake, D.B., 2000. Aquatic feeding in salamanders. In: K. Schwenk (Ed.): Feeding: form, function, and evolution in tetrapod vertebrates, Academic Press, San Diego, pp. 65-94
- Denoël M., 2003. Avantages sélectifs d'un phénotype hétérochronique. Eco-éthologie des populations pédomorphiques du Triton alpestre, *Triturus alpestris* (Amphibia, Caudata). *Cah. Ethol.* 21, 1-327.
- Denoël M., 2004. Feeding performance in heterochronic Alpine newts is consistent with trophic habits and maintenance of polymorphism. *Ethology* 110, 127-136.
- Denoël M., 2007. Le Triton alpestre, *Triturus alpestris* (Laurenti, 1768). In: Jacob J. P., Percsy C., De Wavrin H., Graitson E., Kinet T., Denoël M., Paquay M., Percsy N., Remacle A. (Eds), Amphibiens et Reptiles de Wallonie. Aves-Rainne & Région wallonne, Namur, pp. 62-71.
- Denoël M., Andreone, F., 2003. Trophic habits and aquatic microhabitat use in gilled immature, paedomorphic and metamorphic Alpine newts (*Triturus alpestris apuanus*) in a pond in central Italy. *Belg. J. Zool.* 133, 95-102.
- Denoël M., Hervant, F., Schabetsberger, R., Joly, P., 2002. Short- and long term advantages of an alternative ontogenetic pathway. *Biol. J. Linn. Soc.* 77, 105-112.
- Denoël M., Joly, P., 2001. Adaptive significance of facultative paedomorphosis in *Triturus alpestris* (Amphibia, Caudata): resource partitioning in an alpine lake. *Freshw. Biol.* 46, 1387-1396.
- Denoël M., Schabetsberger, R., 2003. Resource partitioning in two heterochronic populations of Greek Alpine newts, *Triturus alpestris veluchiensis*. *Acta oecol.* 24, 55-64.
- Denoël M., Whiteman, H.H., Wissinger, S.A., 2006. Temporal shift of diet in alternative cannibalistic morphs of the tiger salamander. *Biol. J. Linn. Soc.* 89, 373-382.
- Denoël M., Whiteman, H.H., Wissinger, S.A., 2007. Foraging tactics in alternative heterochronic salamander morphs: trophic quality of ponds matters more than water permanency. *Freshw. Biol.* 52, 1667-1676.
- Duellman W.E., Trueb, L., 1994. Biology of amphibians, The John Hopkins University Press, Baltimore, MD, 670.
- Dunbar R.I.M., 1982. Intraspecific variations in mating strategy. In: Bateson P.P.G., Klopfer P.H. (Eds), Perspectives in Ethology. Plenum Press, New York, pp. 385-431.
- Estrada A., Rivera, A., Coates-Estrada, R., 2002. Predation of artificial nests in a fragmented landscape in the tropical region of Los Tuxtlas, Mexico. *Biol. Conserv.* 106, 199-209.
- Gibbons M.M., McCarthy, T.K., 1986. The reproductive output of frogs *Rana temporaria* (L.) with particular reference to body size and age. *J. Zool.* 209, 579-593.
- Griffiths R.A., 1996. Newts and salamanders of Europe. T. & A. D. Poyser Natural History, London.
- Griffiths R.A., Mylotte, V.J., 1987. Microhabitat selection and feeding relations of smooth and warty newts, *Triturus vulgaris* and *T. cristatus*, at an upland pond in mid-Wales. *Holarctic Ecol.* 10, 1-7.
- Gross M.R., 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends Ecol. Evol.* 11, 92-98.
- Harrison J.D., 1987. Food and feeding relations of common frog and common toad tadpoles (*Rana temporaria* and *Bufo bufo*) at a pond in Mid-Wales. *Herpetol. J.* 1, 141-143.
- Herrel A., Wauters, I., Aerts, P., de Vree, F., 1997. The mechanics of ovophagy in the beaded lizard (*Heloderma horridum*). *J. Herpetol.* 31, 183-393.
- Heusser H., 1971. Differenzierendes Kaulquappen-Fressen durch Molche. *Experientia* 27, 475-476.
- Hoff K., Blaustein, A.R., McDiarmid, R.W., Altig, R., 1999. Behavior. Interactions and their consequences. In: McDiarmid R.W., Altig R. (Eds), Tadpoles. The University of Chicago Press, Chicago, pp. 215-239
- Houston, W.W.K., 1973. The food of the common frog, *Rana temporaria*, on high moorland in northern England. *J. Zool.* 171, 153-165.
- Järnegren J., Tobias, C.R., Macko, S.A., Young, C.M., 2005. Egg predation fuels unique species association at deep-sea hydrocarbon seeps. *Biol. Bull.* 209, 87-93.
- Joly P., 1981. Le comportement prédateur du Triton alpestre (*Triturus alpestris*). I. Etude descriptive. *Biol. Behav.* 6, 339-355.
- Joly P., 1987. Le régime alimentaire des amphibiens: méthodes d'étude. *Alytes* 6, 11-17.
- Joly P., Giacoma, C., 1992. Limitation of similarity and feeding habits in three syntopic species of newts (*Triturus*, Amphibia). *Ecography* 15, 401-411.
- Kaplan R.H., Sherman, P.W., 1980. Intraspecific oophagy in Californian newts. *J. Herpetol.* 14, 183-185.
- Komoroski M.J., Congdon, J.D., 2001. Scaling of nonpolar lipids with ovum size in the mole salamander, *Ambystoma talpoideum*. *J. Herpetol.* 35, 517-521.
- Komoroski M.J., Nagle, R.D., Congdon, J.D., 1998. Relationships of lipids to ovum size in amphibians. *Phys. Zool.* 71, 633-641.
- Kudo S.-I., Nakahira, T., 2004. Effects of trophic-eggs on offspring performance and rivalry in a sub-social bug. *Oikos* 107, 28-35.
- Kuzmin S.L., 1990. Trophic niche overlap in syntopic postmetamorphic amphibians of the Carpathian Mountains (Ukraine: Soviet Union). *Herpetozoa* 3, 13-24.
- Kwet A., 1996. Zu den natürlichen Feinden des Laichs von Froschlurchen. *Salamandra* 32, 31-44.
- Loman J., 1979. Food, feeding rates and prey-size selection in juvenile and adult frogs, *Rana arvalis* Nilss. and *R. temporaria* L. *Ekol. Polska* 27, 581-601.

- Loman J., 2001. Effects of tadpole grazing on periphytic algae in ponds. *Wetlands Ecol. Manag.* 9, 135-139.
- Martin E., 1982. Distribution des activités comportementales chez le Triton alpestre *Triturus alpestris* (Amphibien, Urodèle) en phase aquatique: étude de la variabilité interindividuelle et de l'intensification locale. PhD Thesis, Université Claude Bernard Lyon 1, 237.
- Miaud C., 1993. Predation of newt eggs (*Triturus alpestris* and *T. helveticus*) - Identification of predators and protective role of oviposition Behavior. *J. Zool.* 231, 575-582.
- Ochi H., Sato, Y., Yanagisawa, Y., 1999. Obligate feeding of cichlid eggs by *Caecomastacembelus zebratus* in Lake Tanganyika. *J. Fish Biol.* 54, 450-459.
- Pfennig D.W., Collins, J.P., 1993. Kinship affects morphogenesis in cannibalistic salamanders. *Nature* 362, 836-838.
- Reading C.J., 1990. Palmate newt predation on common frog, *Rana temporaria*, and common toad, *Bufo bufo*, tadpoles. *Herpetol. J.* 5, 462-465.
- Rulik M., 1993. Contribution to the knowledge of the diet of the newt, *Triturus alpestris*. *Folia Zool.* 42, 33-45.
- Sattmann H., 1989. Über die Nahrung des Bergmolches, *Triturus alpestris* (Laurenti, 1768), in der aquatischen Phase (Caudata: salamandridae). *Herpetozoa* 2, 37-49.
- Scanlon J.D., Shine, R., 1988. Dentition and diet in snakes: adaptations to oophagy in the Australian elapid genus *Simoselaps*. *J. Zool., Lond.* 216, 519-528.
- Schabetsberger R., 1994. Gastric evacuation rates of adult and larval Alpine newts (*Triturus alpestris*) under laboratory and field conditions. *Freshw. Biol.* 31, 143-151.
- Semlitsch R.D., 1985. Reproductive strategy of a facultatively paedomorphic salamander *Ambystoma talpoideum*. *Oecologia, Berl.* 65, 305-313.
- Sokal R.R., Rohlf, F.J., 1995. *Biometry*. Freeman and Co. New York.
- Statsoft-France, 2005. *Statistica* (logiciel d'analyse de données), version 7.1. Maisons-Alfort.
- Stephens D.W., Krebs, J.R., 1986. *Foraging theory*. Princeton University Press. Princeton.
- Stoch F., Dolce, S., 1984. Alimentazione e rapporti alimentari di *Triturus alpestris alpestris* (Laur.), *Triturus cristatus carnifex* (Laur.) e *Triturus vulgaris meridionalis* (Boul.). *Quaderni E.T.P. Udine* 9, 17-28.
- Walters B., 1975. Studies of interspecific predation within an amphibian community. *J. Herpetol.* 9, 267-279.
- Whiteman H.H., Sheen, J.P., Johnson, E.B., VanDeusen, A., Cargille, R., Sacco, T.W., 2003. Heterospecific prey and trophic polyphenism in larval tiger salamanders. *Copeia* 2003, 56-67.
- Zahn A., 1997. Untersuchungen zum *Rana* kl. *esculenta* - *lessonae* Komplex in Oberbayern. *Salamandra* 33, 79-88.

Article history:

Received 20 November 2007

Accepted 28 March 2008

Published online 27 May 2008

DOI: 10.1016/j.actao.2008.03.004