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The presence of common frogs (*Rana temporaria*) increases the body condition of syntopic Alpine newts (*Ichthyosaura alpestris*) in oligotrophic high-altitude ponds: benefits of high-energy prey in a low-productivity habitat

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In low-productivity, high-altitude habitats food can become a limiting factor for the occurring amphibians. Common frog eggs deposited in ponds and the developing tadpoles represent energy-rich prey for syntopic Alpine newts that should be advantageous for storing sufficient amounts of energy to survive hibernation and breed the following spring. In our study population in the Zillertal Alps, Austria at 2100 m a.s.l., in two consecutive years we found the body mass of Alpine newts to be significantly higher in ponds containing tadpoles of the common frog than in ponds without tadpoles. As the frogs forage mostly on land, we regard their eggs as an allochtonous nutrient subsidy for ultra-oligotrophic high-altitude ponds that may have a profound effect on the fitness and distribution of Alpine newts and common frogs.

Introduction

Acquisition of sufficient amounts of energy is a key factor for an animal's survival and fitness. The availability of food may therefore become a limiting factor for organisms in harsh environments such as high-altitude habitats characterised by low temperatures, low nutrient availability, and a short vegetation period (Nagy & Grabherr 2009). Alpine waterbodies for instance, can strongly rely on allochthonous nutrient input (Polis *et al*. 2004), as low temperatures can hinder primary production, and, depending on the bedrock (e.g. granite or gneiss erode slowly providing few minerals), melting snow and rainwater may be the prime sources of nutrients (Keddy

2010). The lower the productivity of a habitat, the more pronounced differences in nutrient availability should be, making such habitats particular suitable to study the effects of energy-rich prey on population productivity. Amphibians inhabiting cold high-altitude habitats need to store sufficient amounts of energy during the short summer months to survive the long winter dormancy and to reproduce in the following spring (Jørgensen 1992, Chen *et al*. 2011). Therefore, obtaining enough nutritious prey to support metabolic needs as well as gamete production should be a key factor for their fitness.

The energetically most profitable prey items for Alpine newts (*Ichthyosaura alpestris*) are probably anuran eggs and tadpoles because they combine high nutritional benefit with low processing costs (Grayson *et al*. 2005, Denoël & Demars 2008). The Alpine newt occurs as top predator in naturally fishless high-altitude alpine ponds (Schabetsberger & Jersabek 1995) in Austria, often in sympatry with the common frog (*Rana temporaria*, Cabela *et al*. 2001). Common frogs belong to the so-called explosive breeders in which all breeding individuals arrive at the spawning site almost synchronously and spawning takes only a few days to weeks (Wells 2007). Male frogs establish large breeding aggregations, which the females join whenever they are ready to spawn. Egg clutches are deposited in dense accumulations that may contain up to 80 spawn clumps per m^2 (Nöllert & Nöllert 1992, MS pers. obs.). Alpine newt diet has been analysed in numerous studies from various habitats and proved to be quite diverse (e.g. Sattmann 1989, Rulik 1993, Schabetsberger & Jersabek 1995, Denoël *et al*. 2004, Kopecký *et al*. 2012). When anuran eggs and larvae are available, they can make up a significant amount of newt stomach content and provide more biomass intake than other prey categories (Sattmann 1989, Denoël & Demars 2008). Common frogs enter their spawning sites immediately after thawing, slightly before newts do, and their eggs are available in large quantities when aquatic prey organisms such as arthropod larvae are still scarce (Schabetsberger & Jersabek 1995).

An animal's foraging success and energy stores can be estimated non-invasively by estimating its body condition from body size and mass data (Jakob *et al*. 1996, Stevenson & Woods 2006). In anuran and urodele amphibians, an index for body condition has successfully been used to investigate differences in food availability and habitat quality (Denoël *et al*. 2002, Pope & Matthews 2002, Sztatecsny & Schabetsberger 2005, Bancila *et al*. 2010, Janin *et al*. 2011, MacCracken & Stebbings 2012). By comparing Alpine newts from ponds with and without tadpoles, we test the hypothesis that the presence of nutritious prey in high altitude oligotrophic breeding sites increases their body condition and discuss possible consequences on fitness. As we observed newts feeding on frog eggs and tadpoles in the field (*see* also Sattmann 1989, Denoël & Demars 2008, Kopecký *et al*. 2012), we refrained from performing diet analysis.

Material and methods

The Alpine newt is widespread in Europe and in Austria it occurs from 300 m up to an altitude of 2100 m a.s.l. (Cabela *et al*. 2001). In high-altitude populations, individuals grow slowly and reach an age of almost 30 years (Schabetsberger *et al*. 2001, Wagner *et al*. 2011). Alpine newts migrate to their breeding ponds slightly later than the frogs (mid May to the beginning of June at ca. 2000 m a.s.l., Sztatecsny & Hödl 2009), and feed heavily on frog egg clutches and small tadpoles where available (MS pers. obs.). Mating starts almost immediately after immigration and females begin egg laying one to two days after mating by wrapping their eggs individually in leaves of aquatic plants or attaching them to organic debris over the course of ca. one month (Rafinski & Osikowski 2002). We carried out our field work in Zemmgrund Valley, Zillertal Alps, Austria (47.028°N, 11.821°E) at an altitude of 2100 m a.s.l. where a number of tarns and fens on Gneis bedrock (Wyss 1993) are used as breeding sites by Alpine newts and common frogs. The duration of the aquatic phase for newts in our study area depends largely on winter snow levels, as melting snow is the prime source of water for tarns. In years with little precipitation, shallow pools dry out in mid-July (MS pers. obs), whereas at least the larger ponds are permanent. Between 7 and 9 July 2010, and between 10 and 12 July 2011, we surveyed 10 and 16 ponds respectively for occurring Alpine newts and tadpoles of the common frog (Table 1). At the time of our study, all frog tadpoles had hatched and egg clutches were no longer visible, except in a high elevation breeding pond at 2460 m not inhabited by Alpine newts. In 2011, we additionally measured size and maximum depth of each pond as well as conductivity and maximum water temperature ca. 10 cm below the water surface with a multi-parameter electrode (HI 98129, Hanna Instruments, USA). As water temperature varies during the day, we took our measurements from all ponds within 40 minutes starting at 15:00 on 12 July 2011. From each pond, we captured as many newts as possible using a dipnet and measured their snout–vent length (SVL) with a ruler to the nearest 1 mm, and their body mass (BM) to the nearest 0.01 g using a digital mini scale (Weighcom e68, Eong Huat, Malaysia). To assess body condition, we regressed SVL (log-transformed) and BM (log-transformed), a method proved to predict fat stores in Alpine newts (Denoël *et al*. 2002; but *see* Peig & Green 2009 for higher vertebrates). We performed a Linear Mixed Model (LMM) with restricted maximum likelihood (REML) in which BM was treated as a dependent variable; while SVL, the presence of tadpoles, sex, and the interaction of sex and tadpoles were entered as fixed effects, and pondID as a random effect in order to reproduce the design of the experiment in the model. The analysis was performed using the nlme package within the R statistical software, ver. 2.15.2 (R Development Core Team 2012).

Results

In 2010, we captured 85 male and 58 female Alpine newts from 10 ponds and in 2011, 145 males and 60 females from 16 ponds. Sex ratios were male-biased in most ponds but ranged from 1.25–0.08 female/male (Table 1). In both years, the same four ponds contained tadpoles of the common frog, and from these ponds we captured a total of 44 and 49 newts in 2010 and 2011, respectively. Ponds containing frog tadpoles did not differ from those without tadpoles in any parameter (Mann-Whitney *U*-test: $p > 0.8$ in all cases, *see* also Table 1). The effect of SVL on BM was significant and SVL was therefore always included as a confounding variable. BM of Alpine newts was significantly affected by the presence of tadpoles in both years (LMM 2010 tadpoles: $\beta = 0.105$, SE = 0.019, $t = 5.357$, $p < 0.001$; LMM 2011 tadpoles: $\beta = 0.069$, SE = 0.018, $t = 3.673$, $p = 0.003$, Fig. 1). Female newts showed a greater increase in BM in the

Table 1. The presence of common frog tadpoles, conductivity, water temperature, maximum depth, and Alpine newt sex ratio (females/males) in 16 study ponds.

Pond ID	Tadpoles	Conductivity (μS m^{-1})	Temperature (°C)	Size (m^2)	Depth (m)	Sex ratio
1	absent	2.5	23.76	45.6	0.43	0.50
2	present	1.0	21.70	279.4	1.2	0.25
3	absent	1.5	22.63	700.0	0.6	0.15
4	present	5.0	25.40	40.8	0.31	0.29
5	present	7.0	25.50	28.0	0.25	0.21
6	present	6.0	26.53	5.0	0.22	1.25
7	absent	6.0	27.56	28.5	0.28	0.08
8	absent	1.5	27.36	31.9	0.24	0.57
9	absent	9.5	20.73	116.4	1.39	0.63
10	absent	8.0	22.30	193.2	0.6	1.00
11	absent	1.0	26.83	8.3	0.12	0.20
12	absent	4.0	29.20	160.2	0.22	0.20
13	absent	2.0	24.13	10.1	0.41	1.50
14	absent	2.0	23.80	25.4	0.25	0.17
15	absent	3.0	25.16	27.5	0.27	0.14
16	absent	1.5	26.30	25.4	0.34	0.17

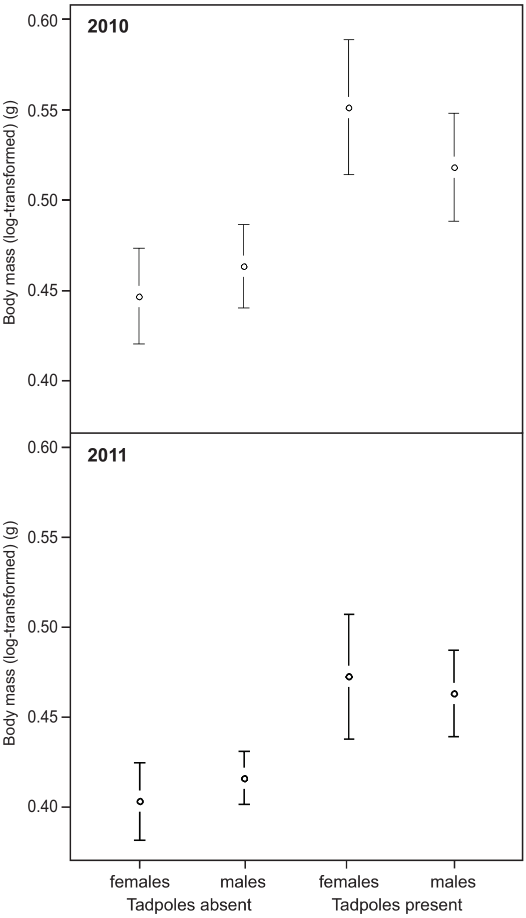

Fig. 1. Sex-specific mean body mass (circles) ± 95% confidence limits of Alpine newts from ponds containing tadpoles of the common frog (four ponds in both years) and from ponds without tadpoles (six ponds in 2010 and 12 ponds in 2011) as derived from LMM.

presence of tadpoles than males but the effect was significant only in 2010 (LMM 2010 sex × tadpoles: β = –0.050, SE = 0.020, t = –2.45, p = 0.026; LMM 2011 sex × tadpoles: β = –0.022, SE = 0.020, t = –1.139, p = 0.256, Fig. 1). Newt sex did not affect BM (LMM 2010 sex: β = 0.013, SE = 0.012, t = 1.027, p =0.306; LMM 2011 sex: β = 0.017, SE = 0.018, t = 0.901, p = 0.369).

Discussion

Despite the small sample sizes, our results showed a significant effect of the presence of common frogs on the body condition of Alpine newts. As we could not find any other difference between our study ponds, the previously present frog eggs and the detected tadpoles likely served as a nutritious prey increasing BM of the newts. There is some indication that female newts may forage more on amphibian eggs than males (Sattmann 1989, Marshall *et al*. 1990, Kopecký *et al*. 2012) or respond more quickly to changing food availability (Denoël & Poncin 2001), which might explain the greater effect of common frog presence on BM in females in 2010. Energetic demands imposed by reproduction are greater for females than for males (Wells 2007). Egg production may take up to 48% of a female's total energy budget (Fitzpatrick 1973), and egg wrapping may also add to the cost. Costs for males are mostly associated with searching for females and performing the mating display. Newts may easily replenish fat deposits depleted by reproduction if food is not limited. At high altitudes, however, the activity period available to restore energy reserves is short before animals enter hibernation, which can last up to eight months (Wells 2007). The amount of available food determines energy assimilation and can affect growth, lipid levels, clutch size and the probability to reproduce in salamanders (Scott & Fore 1995).

Other factors that might explain differences in BM include hydration of newts, the number of unlaid eggs remaining, and the gut content of an individual at the time of weighing. Skin permeability increases when newts enter the breeding pond, facilitating the uptake of water (Lodi *et al*. 1982) and thus leading to an increase in body mass (Verrell & Halliday 1985). As we took our measurements at least six weeks after the newts had entered the aquatic phase, hydration differences should have no longer been relevant. The timing of our study should also have reduced differences in the number of eggs that remained within the females' body cavity as egg laying in Alpine newts takes about four weeks or a bit longer (Rafinski & Osikowski 2002), and females had likely laid all eggs at the time of our study. In case the recorded differences in BM were a consequence of higher biomass in the newts' stomachs, this should later transfer into higher energy reserves not affecting our results. We also detected larvae of Trichoptera, Megaloptera and Chironomidae, as well as nauplii of Copepods in the study ponds, but given that tadpoles were the dominant food resource in these ultra-oligotrophic tarns, we consider it unlikely that other prey caused differences in stomach fullness. Unfortunately it remains unknown whether only the ponds in which we detected tadpoles had originally contained frog egg clutches. The possibility remains that newts had foraged on all frog eggs prior to our study in some ponds, and tadpoles could only be found where a high number of female frogs had spawned.

Common frog egg clutches contain, on average, 1000 eggs (Gibbons & McCarthy 1986), and were shown to increase the newts' biomass uptake (Denoël & Demars 2008). As common frogs were not present in all ponds, our newt study population appears to be distributed over two distinct habitat patches: ponds in which nutrient-rich prey occurs and ponds from which it is absent. As the additional prey might lead to a fitness advantage in newts, while newt predation reduces frog reproductive output, the two types of ponds might correspond to source and sink habitat patches within a two-species metapopulation framework (Holt 1985). Ponds containing both species are likely to be sinks for frogs, and the necessary surplus of individuals to stabilize predator–prey interactions might originate from habitat patches inaccessible or less suitable for predators (Amarasekare 2003, Sepulveda & Lowe 2011). For instance, common frogs are more agile than newts and can utilize ponds in steep terrain out of reach for newts, or temporary ponds that dry up too early for newt larvae to complete metamorphosis (but *see* Denoël *et al.* 2007). To answer questions on distribution and interaction of the two species, data on site selection and fidelity as well as dispersal would be needed.

As common frogs spend most of their life cycle on land (Nöllert & Nöllert 1992), the energy stores used to produce eggs originate to a large degree from the terrestrial habitat. When frogs spawn, their egg clutches therefore constitute an allochthonous nutrient subsidy for the aquatic habitat. While feeding on empneuston (i.e. organic matter) as another terrestrial energy subsidy is important in larger lake ecosystems (Denoël & Schabetsberger 2003, Mehner *et al.* 2005), the biomass of exogenous terrestrial insects blown on to the water surface of small alpine ponds is low as compared with that of anuran eggs. Energy and nutrients moving across habitat boundaries may have important implications for the receiving system (Polis *et al.* 2004). There are examples for energy exchange between terrestrial and aquatic habitats (Schindler & Scheuerell 2002), but to our knowledge eggs deposited by mostly terrestrial animals in an aquatic habitat have not yet received much attention as energy subsidy. The next step would be to test if the predicted fitness advantage of newts results in laying more or larger eggs or being able to reproduce more frequently and at a younger age. Another question arising from our study is whether the prey–predator interaction influences the altitudinal distribution of Alpine newts and common frogs. Newts may strongly reduce the reproductive success of frogs but at the same time may require eggs and tadpoles as nutritious prey to reproduce themselves.

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