

Individual trophic specialisation in the Alpine newt increases with increasing resource diversity

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Received 19 Sep. 2018, final version received 14 Nov. 2018, accepted 16 Nov. 2018

Salvidio S., Costa A. & Crovetto F. 2019: Individual trophic specialisation in the Alpine newt increases with increasing resource diversity. — *Ann. Zool. Fennici* 56: 17–24.

Dietary studies suggest that amphibians are opportunistic predators. However, there is little information on the ability of individuals to change their feeding strategy in time because most studies do not evaluate prey availability and its effect on individual behaviour. To better understand how variation in prey availability may affect the feeding strategy of newts, we studied the Alpine newt, *Ichthyosaura alpestris*, during April and June in 2015, when we monitored prey availability and the species dietary habits. In April at low prey diversity, the newts were generalists, i.e., their diet overlapped almost completely with prey availability. In June when prey diversity was high, the newts became specialists. At the individual level, 9 out of 15 recaptured newts shifted from a generalist to a specialist feeding strategy from April to June, suggesting a rapid behavioural change in response to increasing prey diversity, in accordance with optimal foraging theory. These results stress the importance of sampling the same individuals several times during an extended period of time to better understand the patterns of diet variation in amphibians.

Introduction

Populations of generalists are often composed of specialized individuals having a reduced niche as compared with the one representative for the entire population (Bolnick *et al.* 2002, 2003, Araujo *et al.* 2011). In the case of a trophic niche, the contribution of specialized individuals to the overall feeding strategy can be estimated by analysing dietary habits of an adequate number of individuals sampled exactly at the same time (i.e., cross-sectional analysis), or by resampling the same individuals at different times. Both methods allow to better understand the impact of individual behaviour on the popu-

lation realized trophic niche and have been used to study different species of predators acting at different levels of the food chain (e.g., Bolnick *et al.* 2002, Araujo *et al.* 2011, Novak & Tinker 2015, Pagani-Núñez *et al.* 2016).

Trophic specialization at the individual level is well recognized in many animal species and has been detected in several post-metamorphic amphibian populations (e.g., Araujo *et al.* 2009, da Rosa *et al.* 2011, Schriever & Williams 2013, Costa *et al.* 2015, Salvidio *et al.* 2015). Adult amphibians are generally considered opportunistic predators that feed on many different prey taxa, usually in proportions similar to those in the environment (e.g., Solé & Rödder 2010). In

any case, environmental conditions and available prey are not constant through time, and behavioural responses may change accordingly, both at the population and at the individual levels (Devictor *et al.* 2010, Pagani-Núñez *et al.* 2016). Therefore, the population's feeding strategy should be evaluated in time, possibly considering the behavioural response of the same individuals, in particular to assess how constant their individual trophic response to changing prey resources is. However, in the case of Amphibians, only cross-sectional studies were performed to understand the contribution of an individual to the overall population feeding strategy (e.g., Araujo *et al.* 2009, da Rosa *et al.* 2011, Schriever & Williams 2013, Costa *et al.* 2015, Salvidio *et al.* 2015), while studies over extended periods of time are still lacking. This lack of information is probably caused by the small size and cryptic behaviour of many amphibians that are difficult to observe in the wild. In addition, recapturing and recognizing amphibian individuals may be challenging and time consuming, although natural patterns can be exploited and several artificial marking techniques, with low impact on animal health and well-being, are now available (Ferner 2010).

To fill this gap, in April and June 2015 we gathered data for a wild newt population living in a simplified habitat. In the present study we sampled an Alpine newt population breeding inside a tank holding water for irrigation. In this natural "mesocosm", we sampled the newts and their available trophic resources two times during the same breeding season, to understand short-term variations in population feeding strategy in relation to the changes in prey availability. First, we investigated how temporal variation in prey availability affects newt foraging behaviour, both at the population and individual levels. In case of a significant variation in prey diversity, we expected that the newts would become more specialized in agreement with the classical theory of optimal foraging strategy (Stephens & Krebs 1984). Second, we studied potential differences in individual feeding strategies between male and female newts during their breeding season. Here we expected some variations in feeding behaviour to exist between males and females, because intersexual dietary differences

were observed in a population of the Alpine newt, sampled in the Czech Republic during the breeding period (Kopeky *et al.* 2012).

Material and methods

Study species and site

The studied Alpine newt population belongs to the Italian Apennine subspecies *Ichthyosaura alpestris apuanus*. This subspecies is found in Italy and is distributed from the Maritime Alps to the Central Apennines, and from the sea level up to about 1800 m a.s.l. (Andreone *et al.* 2007). During the aquatic phase, the species' diet includes mainly benthic and planktonic invertebrates, terrestrial invertebrates that fell on the water surface, and also amphibian eggs (e.g., Fasola 1993, Schabetsberger & Jersabek 1995, Denoel & Andreone 2003). The diet composition in different populations indicates high variability related to habitat, season and morph type (larvae, pedomorphs and metamorphosed adults) (Fasola 1993, Schabetsberger & Jersabek 1995, Denoel & Andreone 2003, Vignoli *et al.* 2007, Sanchez-Hernandez 2014). In particular, adults are usually found along pond shores and near the water surface where they prey opportunistically on terrestrial invertebrates (Denoel *et al.* 2004, Vignoli *et al.* 2007). Regarding differences in the diet between sexes, recent studies gave contrasting results. For instance, Lejeune *et al.* (2018) analysing both stomach contents and stable isotopes showed no differences between male and female diets in the French Alps, while Kopeky *et al.* (2012) found that, in a Czech Republic population, females consumed more prey items and more prey categories than males. However these results are not mutually exclusive, because the two studied ecosystems were very different and, in addition, the Czech population was sampled during its entire breeding period (Kopeky *et al.* 2012), while the French one only at the end of its reproductive season (Lejeune *et al.* 2018).

Our study site is located 300 m a.s.l. in the municipality of Santo Stefano Magra, Province of La Spezia, Liguria (NW Italy). In the study area, the Alpine newt breeds in natural and artificial standing waters during spring (Andreone

& Doré 1992, Andreone *et al.* 2007), and in rural landscapes this amphibian is often found in tanks holding water for irrigation (Romano *et al.* 2014). At our study site, there is a tank holding water for irrigation whose dimensions (length \times width \times height) are approx. $3 \times 1.5 \times 1$ m. The water to fill the tank is drawn from a nearby stream: newts occur both in the stream pools and in the water tank but are more abundant in the latter. In Mediterranean permanent water habitats, paedomorphic populations of the Alpine newt are sometimes present (Andreone *et al.* 2007), but they were not observed at the study site. Therefore, our study was based only on adult metamorphosed newts.

Sampling and data analysis

Newts were sampled on 26 April and 4 June 2015. Their diet was evaluated by stomach flushing (Fraser 1976), a non-lethal and highly reliable technique in amphibians and in particular in salamanders (Crovetto *et al.* 2012, Costa *et al.* 2014). Flushed animals were immediately released, and no mortality was observed. Newts were sexed on the basis of their secondary sexual characters, such as the presence of a dorsal crest, and blue colouration in adult males (Andreone *et al.* 2007). In addition, the spotted gular pattern typical for this subspecies (Andreone *et al.* 2007) was photographed to allow for later individual recognition. Stomach contents were preserved in the field in 70% ethanol and later analysed under a dissecting microscope in the laboratory. In addition, prey categories available to the newts were sampled in both months by taking six macro-invertebrate samples from the water tank. Invertebrates were collected into a plastic pipe 40 cm in diameter and 80 cm long placed on the bottom of the tank bottom using a Surber-sampler-like net with a 20×20 cm quadrat frame and 0.5 mm mesh. Collected macroinvertebrates preserved in the field in 70% ethanol and later identified in the laboratory.

Individuals with empty stomachs, or with only plant or unidentifiable animal material were excluded from analyses. In addition, stomachs containing only one identified prey item were also removed, to reduce inflation of the

indexes of individual specialization (Bolnick *et al.* 2002).

We compared the overlap between the population diet and prey availability by means of Pianka's symmetric index (Pianka 1973). This index (O_{jk}) varies from 0 when there is no overlap, to 1 when a complete overlap occurs. The numbers of prey items available to the newts and sampled in April and June were compared using a binomial test (Siegel & Castellan 1988).

The diets of the newts sampled in April and June were compared using two-way non-parametric multivariate analysis of variance based on the Bray-Curtis dissimilarity index and 9999 permutations (PERMANOVA; Anderson 2001). Diversity of available prey and of the newts' total niche width (TNW), as defined by Roughgarden (1972) were estimated using Shannon's H' with 95% confidence intervals obtained by 999 permutations. The individual level of specialization was estimated by means of the proportional similarity index (PSi) that measures the overlap between the niche of individual i and the niche of the entire population (Bolnick *et al.* 2002, 2003). The PSi varies from near 0, when the individual's niche overlaps little with that of the entire population, to 1 when a complete overlap is observed. The overall population level of specialization was measured using the individual specialization (IS) index, that is the mean of the PSi individual values (Bolnick *et al.* 2002, 2003). Therefore, a population can be considered specialist when IS assumes low values and generalist when IS approaches 1. Statistical significance of the PSi and IS was assessed by comparison with the null model distribution obtained by 999 Monte Carlo resamplings, in which each individual is reassigned its original number of prey, drawn randomly from the overall dietary sample. To interpret the change in feeding strategy from April to June, we defined the threshold value for a specialist feeding strategy as the lower 95% limit of the confidence interval of the null distribution derived from 999 Monte Carlo resamplings of the original data set (Costa *et al.* 2015).

Trophic indexes and null models were estimated using the IndSpec 1.0 software (Bolnick *et al.* 2002). PSi values and numbers of prey items obtained in April and June for the same

photo-identified individuals were compared by means of Wilcoxon's paired test, that is suited for comparing the same individuals exposed to different conditions without assuming any *a priori* distribution (Siegel & Castellan 1988).

Results

Newts' eggs were present in the stomachs both in April and June, confirming that sampling covered the entire breeding season. We found both aquatic and terrestrial prey categories in the newts' stomachs indicating that Alpine newts fed

opportunistically this kind of prey. The overlap between the population diet and prey availability was almost complete in April ($O_{jk} = 0.94$), while in June it was reduced ($O_{jk} = 0.63$; Table 1).

There was no significant difference between April and June population niche widths (April TNH = 2.01 vs. June TNW = 2.16; $p = 0.369$, after 999 permutations). However, there was a significant difference between the months when prey taxonomic composition was considered (PERMANOVA: $F = 9.6$, $p = 0.001$), with no significant differences for the sex \times month interaction ($F = 1.04$, $p = 0.09$) or between sexes ($F = 1.4$, $p = 0.18$; Table 2).

Table 1. Prey availability and items found in stomachs of newts in April and June. Shannon's diversity index H' corresponds to the total niche width (TNW) of Roughgarden (1972); p = significance level after 999 permutations.

	April		June	
	Prey availability	Stomach contents ($n = 27$)	Prey availability	Stomach contents ($n = 22$)
Aquatic taxa				
Nematoda	8	1	6	0
Turbellaria	0	0	0	10
Oligochaeta	0	0	1	0
Gasteropoda	3	5	4	3
Acarians	10	2	15	0
Anostraca	0	1	0	0
Ostracoda	0	2	0	0
Isopoda	0	0	1	1
Chironomidae larvae	43	60	19	34
Chironomidae pupae	3	2	2	5
Coleoptera larvae	0	2	2	1
Diptera larvae	1	1	2	19
Ephemeroptera larvae	0	2	6	1
Heteroptera	2	9	1	1
Tricoptera larvae	7	6	5	4
Odonata nymphs	3	1	6	5
Newt eggs	0	8	0	2
Terrestrial taxa				
Diplopoda	0	2	1	0
Aranea	0	2	2	2
Aphidoidea	0	2	0	16
Diptera adults	2	5	3	12
Hymenoptera flying adults	0	0	1	0
Hymenoptera Formicidae	4	0	1	0
Orthoptera	0	8	1	0
Total abundance	86	121	79	116
Shannon's H'	1.74	2.01	2.46	2.16
95% CL	1.42–1.93	1.66–2.18	2.12–2.54	1.93–2.26
O_{jk} overlap index	0.94	0.63		
IS (individual specialisation index)	–	0.47	–	0.40
$p \neq$ null distribution		> 0.33		< 0.006

There was a striking difference in the population feeding strategy between April and June samples. The population's IS was not different from the null model in April ($p = 0.332$, after 999 permutations) suggesting that the entire newt population behaved as a generalist predator (Fig. 1). In June, however, the population's IS index indicated a shift towards a more specialist feeding strategy (difference from the null model, $p < 0.006$, after 999 permutations; Fig. 1 and Table 2).

When the diet of the 15 newts captured both in April and June was analysed, the mean number of prey items found in their stomachs was lower in April (mean = 3.53, SD = 0.38) as compared with that in June (mean = 5.20, SD = 0.87), but this difference was not significant (Wilcoxon test: $z = 1.37$, $p = 0.17$), and there was no significant difference when values for males and females were tested separately (Wilcoxon test: $z = 1.71$, $p = 0.09$ and $z = 0$, $p = 1$, for males and females, respectively). The individual PSi values for the 15 newts captured in April and June showed that 9 individuals shifted from a generalist to a specialist feeding pattern (Table 3), and this pattern was significant between months (Wilcoxon-paired test: $z = 2.33$, $p = 0.02$) but not when values for males and females were tested separately (Wilcoxon test: $z = 1.82$, $p = 0.07$ and $z = 0.35$, $p = 0.18$, for males and females, respectively).

Discussion

Our analysis of Alpine newt population feeding strategies gave a clear answer to our first question, concerning the relationship between individual specialization and variation in diversity of available prey. Indeed, the feeding strategy of the newt population clearly changed from generalist in April, when prey diversity was low, towards specialist in June, when available resources were more diverse. This conclusion is based on the data obtained from 15 newts caught in April and recaptured in June.

We found no differences in feeding strategies between males and females. This finding contradicts the results of Kopek \acute{y} *et al.* (2012) and was somehow surprising to us. However, the absence

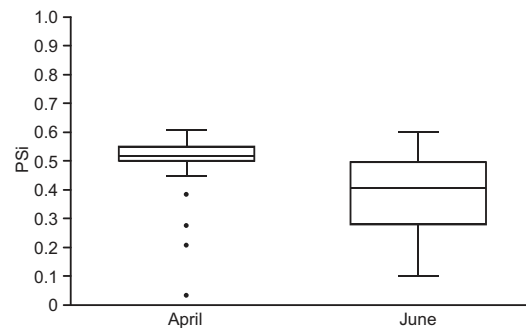


Fig. 1. Box-and-whiskers plot of individual specialization index (PSi) for the same individual newts *Ichthyosaura alpestris* sampled both in April and June. Median: horizontal line inside the box, box: 25–75 quartiles; whiskers: values up to 1.5 times the box height, dots: outliers. Lower PSi values correspond to a higher individual specialisation.

of differences between sexes was based on relatively small samples (only 8 males and 7 females were recaptured; cf. Table 3) and, therefore, it should be studied further on larger samples.

Other findings of our study were that the overall population trophic niche width (TNW) did not change from April to June, while the individual feeding strategy as measured by the PSi did, i.e., a population composed mostly of generalists in April became a population of specialists in June (cf. Fig. 1). This change was caused by a shift in individual feeding behaviour that occurred in a relatively short time (i.e., less than 40 days). There may be several reasons for this shift. For example, increased prey diversity in June. This is not surprising because freshwater Mediterranean ecosystems are greatly affected by seasonality and, in particular, in standing waters macroinvertebrate diversity usually peaks by the end of spring (e.g., Trigal *et al.* 2007). This pattern is in agreement with previous

Table 2. Results of two-way PERMANOVA on April and June newt prey composition samples.

Source	SS	d.f.	MSS	F	p
Month	2.358	1	2.359	9.600	0.0001
Sex	0.341	1	0.341	1.389	0.178
Sex × month	0.255	1	0.254	1.036	0.092
Residual	10.812	44	0.246		
Total	13.766	47			

studies showing that an increase in prey diversity enhances trophic-niche variation within and among populations of predators (e.g., Araujo & Costa-Perreira 2013, Sánchez-Hernández *et al.* 2017). Therefore, during a high prey diversity period, newt individuals actively search for and capture the most beneficial or energetic prey categories found in their habitats, which is in agreement with optimal foraging strategy (Stephens *et al.* 2007). In fact, newt individuals differed in their feeding behaviour by selecting different prey categories, thus increasing individual niche variation (Table 1). Finally, when the individual feeding strategies of the recaptured newts were analysed, it became evident that several of them were capable of rapid shift from generalist to a more specialist feeding behaviour by consuming only few prey categories, when prey diversity in the environment was high. This occurred without an observable change in the number of prey items captured per individual and apparently there was no difference in feeding behaviour between sexes.

This is not the first case of intra-population variation in feeding habits found in amphibians, because similar was already observed in the terrestrial cave salamander *Speleomantes stri-natii* (Salvidio *et al.* 2015). However, there are

two main differences between these two cases: in the terrestrial system studied by Salvidio *et al.* (2015), the population trophic-niche width varied being greater in autumn and smaller in spring, while the population remained specialized at the individual level in both seasons. In the aquatic newt population analysed here, however, the trophic niche width remained constant, while the overall population feeding strategy changed from generalist to specialist in a very short time, a finding that is remarkable both from behavioural and ecological points of view. The mechanisms of the observed shift in population feeding strategy were investigated by comparing trophic niches of the same newt individuals captured in April and recaptured in June. In fact, the majority of individuals shifted from generalist to specialist, sometimes displaying a striking difference in P_{Si} values between April and June ($> |0.20|$; cf. Table 3). These results indicate that individual newts are able to change their feeding behaviour within the same season. This change may be caused by active selection of the hunting microhabitat or by active selection of different prey categories, or both (e.g., Woo *et al.* 2007, Terraube *et al.* 2014). In our current study, the newt habitat was rather homogeneous (a tank holding water for irrigation) and, there-

Table 3. Individual percent similarity values (P_{Si}) of the same individual newts captured in April and recaptured in June. The threshold values corresponding to a specialized strategy were 0.49 and 0.47 for April and June, respectively (cf. Material and methods).

Newt number	Sex	P _{Si}		Difference	Direction of change in trophic strategy
		April	June		
1	male	0.52	0.11	0.40	generalist to specialist
2	male	0.38	0.38	0.00	no change
4	male	0.54	0.48	0.06	no change
6	male	0.50	0.54	-0.04	no change
8	male	0.57	0.24	0.33	generalist to specialist
15	male	0.50	0.54	-0.04	no change
16	male	0.52	0.13	0.39	generalist to specialist
17	male	0.54	0.30	0.24	generalist to specialist
18	female	0.52	0.27	0.25	generalist to specialist
26	female	0.58	0.41	0.17	generalist to specialist
29	female	0.54	0.51	0.03	no change
30	female	0.57	0.13	0.44	generalist to specialist
31	female	0.52	0.47	0.04	generalist to specialist
33	female	0.52	0.46	0.06	generalist to specialist
37	female	0.21	0.52	-0.31	specialist to generalist

fore, a shift resulting from microhabitat selection seems rather improbable, while selective exploitation of different prey types is more convincing. Overall, these findings are in good agreement with the optimal foraging theory, predicting that individual predators will become more selective towards the more beneficial prey, especially during favourable periods when resource diversity is high (Stephens & Krebs 1978, Stephens *et al.* 2007).

Although two of the possible mechanisms causing the observed shift in feeding behaviour were analysed (i.e. the variation in resource diversity and the individual behavioural response to this change), two more factors could also be acting in the study system. The first one is the newt population density, a factor that may affect the feeding strategy of an individual by increasing intra-specific competition for resources available in the shared habitat is observed (Stephens & Krebs 1978, Svanbäck & Bolnick 2007, Svanbäck *et al.* 2011). The second factor that could produce the observed shift is the decrease in abundance of Chiromidae larvae (i.e., main prey category) from April to June. Rarefaction of this prey category could also increase intra-specific competition among individuals foraging for this prey type. Unfortunately we do not have data on newt densities in the two sampling periods and, hence, the possible interaction between variation in trophic resources and predator density in the study ecosystem remains to be tested.

Acknowledgments

Newts were captured under permit 0042466/PNM issued by the Italian Ministry of Environment. Thanks are due to the managing Editor and two anonymous Reviewers that with their constructive comments improved a previous version of this manuscript.

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