FACULTATIVE PAEDOMORPHOSIS IN THE ALPINE NEWT, *TRITURUS A. ALPESTRIS*: FEEDING HABITS AND HABITAT USE IN AN ALPINE LAKE

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Abstract: feeding habits and micro-habitat use were compared between metamorphs and paedomorphs in a population of the Alpine newt, *Triturus a. alpestris* in the French Alps. This population occupies a deep Alpine lake. The paedomorphs largely outnumbered the metamorphs. Whereas paedomorph diet was mainly composed of plankton, that of metamorphs was especially composed of larval and adult insects. The spatial use of the habitat also differed between the two forms: the paedomorphs occupied all the micro-habitats (shore, bottom, water column and surface) while the metamorphs were only found along the shore and at the water surface. In such a deep lake paedomorphosis may have persisted because of a different use of both feeding resources and microhabitat.

KEY WORDS: Paedomorphosis, feeding, habitat use, resource partitioning, Alpine lake, newt.

INTRODUCTION

Heterochrony is suspected to play an important role in both micro- and macroevolutionary processes (Gould, 1977; McKinney and McNamara, 1991). A validation of this hypothesis lies in demonstrating the adaptive advantage that a variation in developmental timing may confer. In this context, the aim of this study was to evidence potential benefits that can be gained by adopting a paedomorphic life history.

Coexistence of several newt species is a common feature of European amphibian communities. In France up to 5 *Triturus* species can live syntopically (Arntzen and De Wijer, 1989). In such assemblages, coexistence is made possible by differences in body size (Joly and Giacoma, 1992), feeding habits (Dolmen and Koksvik, 1983; Fasola and Canova, 1992; Joly and Giacoma, 1992), habitat use (Fasola, 1992; Braz and Joly, 1994), and activity rhythms (Himstedt, 1971). When resources are not limited, newt niches can greatly overlap (Griffiths, 1986, 1987).

European newts are usually amphibiotic,

with aquatic larval period separated from terrestrial juvenile and adult periods by metamorphosis. However, in populations mainly located in Southern Europe not all the larvae transform: some of them retain gills and gill slits, and mature under water as paedomorphs. This trait is known as facultative paedomorphosis (Andreone et al., 1993; Whiteman, 1994). Among other causes, the evolution of such a polyphenism supposes a different feeding niche for the paedomorphs and for the metamorphs. In Italian populations, if no difference in diet was found between the two morphs of the Alpine newt, *Triturus alpestris*, a difference in prey size selection was detected (Fasola and Canova 1992). Prey selection was suspected in another population (Breuil 1986). This study aims at contributing to the question in comparing feeding habits and habitat use between the two forms in a population inhabiting a deep Alpine lake.

Material and Methods

The study site was an Alpine lake (elevation 1950m) located in the Southern French Alps (lac de la Cabane, Alpes-de-Haute-Provence). At highest water level (in June-July), its area reaches 250 x 40 m and its depth 7 m. Macrophytes and fish are lacking. The Alpine newt population (*Triturus alpestris*) was composed of adult metamorphs, adult paedomorphs, and both branchiate and metamorphosed juveniles.

Adult newts were sampled using a landing net in June and July 1997 (15 sampling sessions). Sampling effort was distributed according to a microhabitat x day time design. Four microhabitats were monitored: shore (0-1 m depth), bottom (3-7 m depth, by scuba diving), water column, and surface (using an inflatable dinghy). Each habitat was sampled at dawn, during mid-day and in the evening. Newt stomach contents were gathered following a gut-flushing procedure performed on phenoxy-ethanol anaesthetized animals (Joly, 1987). With respect to gastric evacuation rates (Schabetsberger, 1994), the prey items were flushed just after the newts were collected. All the newts were immediatly released after the experiment. Both morphs and sexes were compared using Mann-Whitney U test (Statsoft, 1996).

Results

Spatial positions of 390 adults among the four habitats were recorded. The paedomorphs outnumbered the metamorphs (they accounted for 78% of the adult population). From these newts, 223 stomach contents were obtained (metamorphs: 27 females and 22 males, paedomorphs: 102 females and 72 males).

Stomach content analysis resulted in the identification of 8065 prey items. Metamorphs and paedomorphs greatly differed in their feeding habits. Paedomorphs preyed significantly more on plankton than did metamorphs, especially concerning *Daphnia,* but also *Chydorus, Chyrocephalus,* Cyclopida and Calanoida. Conversely the metamorphs preyed more on insects: mainly Diptera imagos, but also terrestrial Heteroptera and Coleoptera, and Coleoptera and Plecoptera larvae (Mann-Whitney U test; table 1).

On average, differences between paedomorphs and metamorphs followed the same pattern in males and females. However, no significant differences were found between

	paedomorphs			metamorphs			U-test		
	∑	mean	SE	∑	mean	SE	U	z-adj.	P
Daphnia	5343	30.7	4.8	236	4.8	2.7	1956.5	5.92	<0.001
Chydorus	176	1	0.5	1	0	0	3754.5	2.33	0.02
Polyphemus	43	0.3	0.1	1	0	0	4053	1.30	0.2
Chyrocephalus	257	1.5	0.2	10	0.2	0.1	2723	4.46	<0.001
Cyclopoida	249	1.4	0.7	1	0	0	3139.5	3.87	<0.001
Calanoida	227	1.3	0.3	0	0	0	2866.5	4.57	<0.001
Ostracoda	19	0.1	0.1	2	0	0.2	4131	0.92	0.36
L. Diptera	90	0.5	0.1	23	0.5	0.4	3794.5	1.45	0.15
L. Coleo/Plecoptera	164	0.9	0.1	102	2	0.1	2915	-3.67	<0.001
L. Trichoptera	23	0.1	0	9	0.2	0	4059	-0.89	0.37
Dysticidae imagos	14	0.1	0	4	0.1	0	4213	-0.28	0.78
Bivalvia	5	0	0	0	0	0	4140	1.20	0.23
Lumbricidae	14	0.1	0	8	0.2	1	3889	-1.85	0.06
T. Coleoptera	10	0.1	0	9	0.2	0.1	3873	-2.19	0.03
T. Diptera	453	2.6	0.5	445	9.1	1.4	2382	-5.25	<0.001
T. Heteroptera	16	0.1	0	32	0.7	0.2	3321.5	-4.17	<0.001
T. Hymenoptera	3	0	0	1	0	0	4249.5	-0.15	0.88
T. Pleco./Trichoptera	10	0.1	0	5	0.1	0	4051	-1.26	0.21
Aqua. Invertebrates	27	0.2	0.1	9	0.2	0.1	4232.5	0.15	0.88
T. invertebrates	13	0.1	0	11	0.2	0.1	3939	-1.68	0.09

Tab. 1: Gut contents of the paedomorphs (n = 49) and metamorphs (n = 174): total number, mean per stomach, standard error and Mann-Whitney U test (z-adjusted). Abbreviations: L = larval, T = terrestrial, Aqua. = aquatic.

the males of each morph for *Chydorus* and Cyclopoida (U test).

Whereas the paedomorphic newts occupied all the microhabitats of the lake, the metamorphs were mainly found at the water surface and near the shore (table 2, $\chi^2 = 51.68$, 3 df, $p<0.001$). This difference in habitat use was as marked during the day as during the night. The newts were more abundant at the shore from dusk till dawn. They were present at the water surface mainly during the day, when fallen terrestrial invertebrates were available there. However, newt surfacing depended on the absence of waves. Despite the great proportion of planktonic prey in their diet, paedomorphic newts were observed to catch their prey one by one. On the bottom of the lake, the newts were observed either waiting for prey they just sucked in when close to their mouth, or pursuitting them.

	microhabitat			
newt category	column	bottom	shore	surface
paedomorphs	77	66	129	33
metamorphs	7	1	67	7

Tab. 2: Microhabitat use by the newts of the Lac de la Cabane in June-July 1997 ($\chi^2 = 51.68$, 3 df, $p<0.001$).

DISCUSSION

In the studied population, paedomorphs largely outnumbered metamorphs, and this for several years (Breuil, 1986; pers. obs.). The explanation of such a dominance of paedomorphic newts is to be found in the advantage they took in exploiting all microhabitats of the lake: the shore, the bottom, the water column and the water surface, although the metamorphs only occupied the shore and the water surface. Overall, the diet of paedomorphs differed from that of metamorphs in including more planktonic prey and less insects. This difference is partially due to the habitat partition, density of exogenous insects or aquatic insect larvae being low in the water column. In contrast, paedomorphs took advantage of consuming plankton such as Cladocera, Anostraca, Cyclopoida, and Calanoida that became available at depths that metamorphs did not reach while diving. However, paedomorphs were found searching for prey along the shore or at the water surface. Thus in this population paedomorphosis appears adaptive because of a better use of food and habitat. The persistence of metamorphs in such an environment may perhaps be explained by specific advantages such as avoiding increase of density during the partial drying up of the lake in summer or by the drying up itself.

In another site (Apennines, Italy), Fasola (1992) did not find any prey selection between both morphs, but only a differential prey size selection. However, the difference in diet is suspected to be lower in these ponds because of shallowness and unpredictability (pers. obs.). Some authors assumed paedomorphosis to be a response to harsh terrestrial conditions (Sprules, 1974) or to physical constraints of the aquatic environnement such as low temperature (Bizer, 1978), particular ionic concentration (Gabrion et al., 1978) or low lighting (Svob, 1965). These factors may have an influence on the expression of paedomorphosis but they fail in explaining its recurrent expression in a wide range of aquatic and terrestrial habitats (Breuil, 1992; pers. obs.). Some experimental studies carried out in the 80's have shown that paedomorphosis may also be promoted in permanent waters where newt density is low (Harris, 1987; Semlitsch, 1987). Therefore the expression of paedomorphosis appears to depend on several factors.

If paedomorphs cope well with deep Alpine lakes, why are paedomorphic populations so rare in the Alps? By analyzing allozyme data in the Lac de la Cabane population, Breuil (1986) found a possible genomic introgression by the genome of the subspecies *Triturus alpestris apuanus.* This Italian subspecies occupies the Apennines. A few other populations located in the vicinity of the Lac de la Cabane also contain paedomorphs (Tron, 1995; pers. obs.) and may also have been colonized by Italian Alpine newts. In the Lac de la Cabane the newts also share a morphological trait with *T. a. apuanus:* a large number of dots on the throat. As paedomorphosis is relatively common in Italy and is exceptional outside this country -except in the Balkans (Breuil, 1986), we assume paedomorphosis in Lac de la Cabane to be related to the apuanus genome which would have appeared before or during the Pleistocene glacial period. Such cold events were also associated with paedomorphosis in fossil organisms (Rocek, 1995). Thus paedomorphosis in the Alpine newt has probably a genetical basis, as in salamanders genus Ambystoma (Semlitsch and Wilbur, 1989; Voss, 1995). The persistence of paedomorphic populations would then depend on long-term interactions between potential genes and favourable ecological conditions. Thus the paedomorphic newts from the Lac de la Cabane were favoured by their feeding and spatial niche advantages. The investigation of the ecology of paedomorphosis in other populations will make it possible to improve our theoretical understanding of the evolution of heterochrony.

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