Microhabitat selection and feeding relations of smooth and warty newts, Triturus vulgaris and T. cristatus, at an upland pond in mid-Wales

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Griffiths, R. A. and 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. – Holarct. Ecol 10: 1–7.

The utilization of microhabitat and food resources by *Triturus vulgaris* and *T. cristatus* was studied in an upland pond in mid-Wales. From April to June *T. vulgaris* was more evenly distributed across the pond than *T. cristatus*, which showed a preference for the middle of the pond and the bottom of the water column. From July to September however, when most *T. vulgaris* had left the pond, *T. cristatus* was evenly distributed within the water column and a much higher proportion was captured around the shorelines. Both species appear to be generalist predators with diets limited by prey size. Zooplankton were the most important prey for *T. vulgaris*, while leeches formed the bulk of the diet of *T. cristatus*. However, *T. cristatus* did not select larger-sized zooplankton than *T. vulgaris*. Large body size therefore enables *T. cristatus* to consume a wider range of prey sizes than *T. vulgaris*. Microhabitat niche overlap was greater than feeding niche overlap between the species.

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1. Introduction

In ecological communities assemblages of similar species may partition three types of resources: space (or habitat), food and time (Schoener 1974). These resources constitute the dimensions of the ecological niche of each species, but may be further subdivided into macrohabitat and microhabitat, food type and food size, and seasonal time and diel time. Partitioning of these resources in herpetofaunal assemblages may come about as a result of competition, predation, physiological constraints, or interactions between two or more of these processes (Toft 1985). In some assemblages patterns of resource partitioning reflect size differences between the component species. A large organism, for example, will generally be able to take larger food items than a small organism which is otherwise morphologically similar.

The present study set out to compare microhabitat selection and feeding relations of the smooth newt, *Triturus vulgaris* (L.) with those of the warty newt, *T. cristatus* (Laurenti). *T. vulgaris* is smaller than *T. cristatus*, but the two species overlap in terms of macrohabitat, and the timing of seasonal and diel activities. Whereas *T. vulgaris* is found in a wide variety of pond habitats, *T. cristatus* is more specialized, preferring large deep ponds (Smith 1969, Steward 1969, Beebee 1973, Cooke and Frazer 1976), and is only occasionally found in the absence of *T. vulgaris* (Bell 1979, Prestt et al. 1974, Cooke and Frazer 1976). Where they do coexist, *T. vulgaris* is nearly always more abundant than *T. cristatus* (Bell 1979, Glandt 1978, 1982). In terms of seasonal time, *T. cristatus* spends a longer period in the aquatic habitat (Persson 1946, Smith 1969, Blab and Blab 1981) and on the diel scale is more nocturnal than the mainly crepuscular *T. vulgaris* (Dolmen 1983a, Griffiths 1983).

Dolmen (1983b) observed microhabitat selection under semi-natural conditions and found that *T. cristatus* was more of a bottom-dweller than *T. vulgaris*. Field data is lacking on microhabitat differences, although *T. cristatus* is reported to prefer the deeper, central areas of ponds (Cooke and Frazer 1976). Comparative studies of feeding in the two species suggest that *T. cristatus* consumes somewhat larger prey than *T. vulgaris* (Avery 1968), and that diet may be related to microhabitat selection within the pond (Dolmen and Koksvik 1983).

The present study investigated feeding relations and microhabitat selection in the field simultaneously, and thus allows an assessment of the relative importance of resource partitioning along these two niche dimensions.

2. Material and methods

2.1. The study area

Upper House pool (National Grid reference: SO 078 569) has a surface area of about 400 m², is situated at a height of 360 m, and is surrounded by unimproved upland grassland. Pond water pH is about 7.0, and during the study period of March–September, the temperature of the pond varied from 2°C (March) to 17°C (July). The shoreline is unvegetated for most of the year, but the central area of the pond contains submerged vegetation and is dominated by *Ranunculus peltatus* Schrank and *Apium inundatum* (L.) Reichenb. fil. Along one side of the pond this grades into an area of swamp and emergent vegetation, consisting of *Juncus effusus* L. and *Myosotis secunda* A. Murray. Part of the swamp is shaded by sallow, *Salix cinerea* L. (Fig. 1). The deepest region of the pond is where the open water area grades into the swamp (area C, Fig. 1). This is about 0.7 m deep during the spring and 0.5 m deep in the summer. Average depth of the open water area is about 0.3 m. In addition to *T. vulgaris* and *T. cristatus*, the pond also contains low numbers of the palmate newt, *T. helveticus* (Razoumowsky).

2.2. Microhabitat selection

Habitat selection by newts within the pond was monitored using a weekly trapping programme from 5 March until 10 September 1985. No adult newts were captured in traps placed in the pond after this period. Newts were captured using the funnel traps described by Griffiths (1985). A broad transect (5 m wide, 15 m long) was established across the pond and traversed the main habitat types available to newts (Fig. 1). Sets of traps were placed at intervals of about 4–5 m across the transect so that the following habitat types were sampled: A: unvegetated zone (shoreline); B: submerged vegetation zone; C: submerged vegetation/emergent vegetation interface zone; D: emergent vegetation (swamp) zone. A set of eight traps was used to sample the deepest area of the pond (area C). Four of these traps were placed just
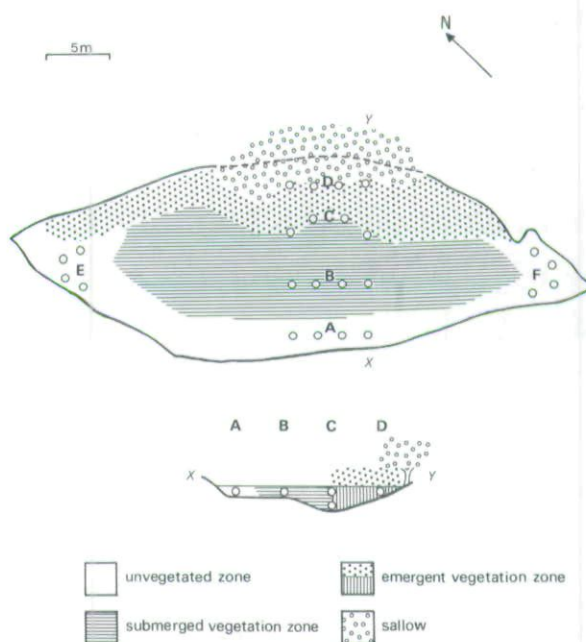

Fig. 1. The study pond. Open circles indicate trap positions and the letters A-F refer to each microhabitat studied.

below the pond surface, with the second four resting on the pond bottom at a depth of 0.5–0.7 m. Areas A, B and D were shallower, and each was sampled with a set of four traps placed on the pond bottom at a maximum depth of 0.3 m. In addition to the transect traps, sets of four traps were also placed in the unvegetated shoreline zones at each end of the pond (areas E and F). Area D became almost dry after 23 July and was therefore omitted on subsequent trapping occasions. Access to each area of the pond was gained by wading, and each week traps were placed in position at 2100 h and emptied at 0900 h the following morning.

Spatial niche overlap between *T. vulgaris* and *T. cristatus* was calculated using Schoener's (1970) index,

$$C = 1 - 0.5 \left(\sum_i |p_{xi} - p_{yi}| \right) \tag{1}$$

where p_{xi} is the proportional utilization of habitat type i by species x, and p_{yi} the proportional utilization of habitat type i by species y. The relative abundances of each species of newt in each of the five habitat types across the transect were used to calculate C, which can vary from 0 (no overlap) to 1.0 (complete overlap).

2.3. Feeding relations

The stomach contents of *T. vulgaris* and· *T. cristatus* were removed by stomach-flushing animals captured in traps in April. This method involves injecting water into the stomach via the mouth, using a syringe equipped with a hypodermic needle covered by plastic tubing. For

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T. vulgaris, the needle was covered with a 34 mm length of 1 mm diameter tubing, and attached to a 1 ml syringe. For the larger *T. cristatus*, a 60 mm length of 1.5 mm diameter tubing was used in conjunction with a 5 ml syringe. Details of the stomach-flushing procedure and its efficiency are described elsewhere (Griffiths 1986). No mortality of newts was observed during or after stomach-flushing, and all stomach-flushed animals were released into the pond within 10 days of capture. Stomach contents were preserved in 70% alcohol with 10% glycerol.

Except for the Chironomidae, which were regarded as being sufficiently distinct to warrant classification to familial level, food items were classified according to order or class. The linear dimensions of the intact items in each prey category were measured. Large invertebrates and frog tadpoles were placed on waxed graph paper and measured to the nearest 0.5 mm. Planktonic organisms were measured to the nearest 0.1 mm using a binocular microscope equipped with an eyepiece graticule. The volume of each prey item was calculated using the formula for an appropriate solid (Appendix). The mean volumes of the different prey types were then calculated and used to estimate the total volume of prey consumed in each prey category.

Estimates of the relative abundances of the different prey items in the pond were obtained by netting the pond in mid-April. In each of the areas A-F three sweeps of a 1 mm mesh dipnet, and three sweeps of a 0.2 mm mesh plankton net were performed. In the deepest area of the pond (area C), successive sweeps sampled the bottom, middle and top of the water column. As both nets had a frame diameter of about 300 mm, approximately the same volume of water was sampled by each net on each sweep. The contents of the two nets were pooled, passed through a 10 mm mesh seive to remove vegetation and other debris, and preserved in 70% alcohol. The procedure for identifying and measuring the prey items was as described above. Overall relative abundances of the different prey categories in the pond were obtained by pooling the data from all the areas of the pond.

Feeding niche overlap between *T. vulgaris* and *T. cristatus* was calculated using equation (1), where p_{xi} is the proportional utilization of prey category i by species x, and p_{yi} the proportional utilization of prey category i by species y. Separate indices were calculated for the numerical and volumetric analyses.

3. Results

3.1. Seasonal dynamics

The first captures of *T. vulgaris* in the pond were made on 12 March, compared to 26 March for *T. cristatus*, indicating a slightly later time of arrival at the pond in the latter species (Fig. 2). The numbers of *T. vulgaris* captured declined through June and none was captured af-
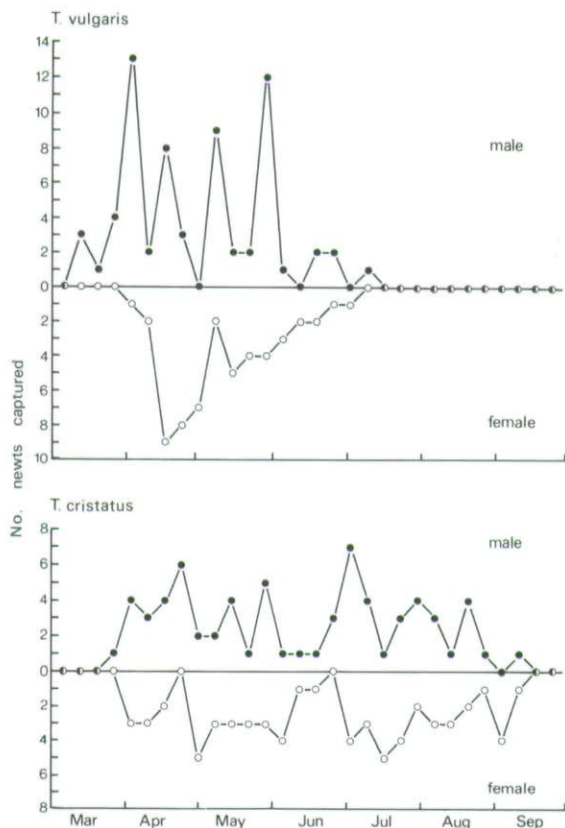

Fig. 2. The total numbers of newts captured in all traps each week during the study period.

ter 9 July. *T. cristatus*, however, had a much longer aquatic period and were captured every week until 10 September. Thus the aquatic period of *T. cristatus* may be divided into two periods: (1) April to June, when *T. vulgaris* were also present in the pond, and (2) July to September, when *T. vulgaris* were mainly absent. Although larvae of both species were also captured in the pond, no subadult newts were observed.

3.2. Microhabitat selection

From April to June, most newts were captured in the central areas of the pond. Across the transect, 56% of *T. vulgaris* and 82% of *T. cristatus* were found in areas B and C (Fig. 3a). In both species, most newts were captured at the open water/emergent vegetation interface. However, in contrast to *T. cristatus*, which displayed an uneven distribution across the pond (Friedman two-way analysis of variance, $\chi_r^2 = 10.47$, $p < 0.05$), the number of *T. vulgaris* captured did not differ significantly between areas ($\chi_r^2 = 6.04$, $p > 0.05$).

The distribution of *T. cristatus* across the pond from July to September was different from that observed earlier in the year, with only 57% of newts being captured in the central areas (Fig. 3a). During this period the

Fig. 3. Microhabitat selection
in *T. vulgaris* and *T. cristatus*.
a, horizontal distribution:
A-D refer to the microhabitats
shown in Fig. 1 (For area C
only data from the pond
bottom is included).
b, vertical distribution in
area C. Sample sizes are
shown at the top of each
column.
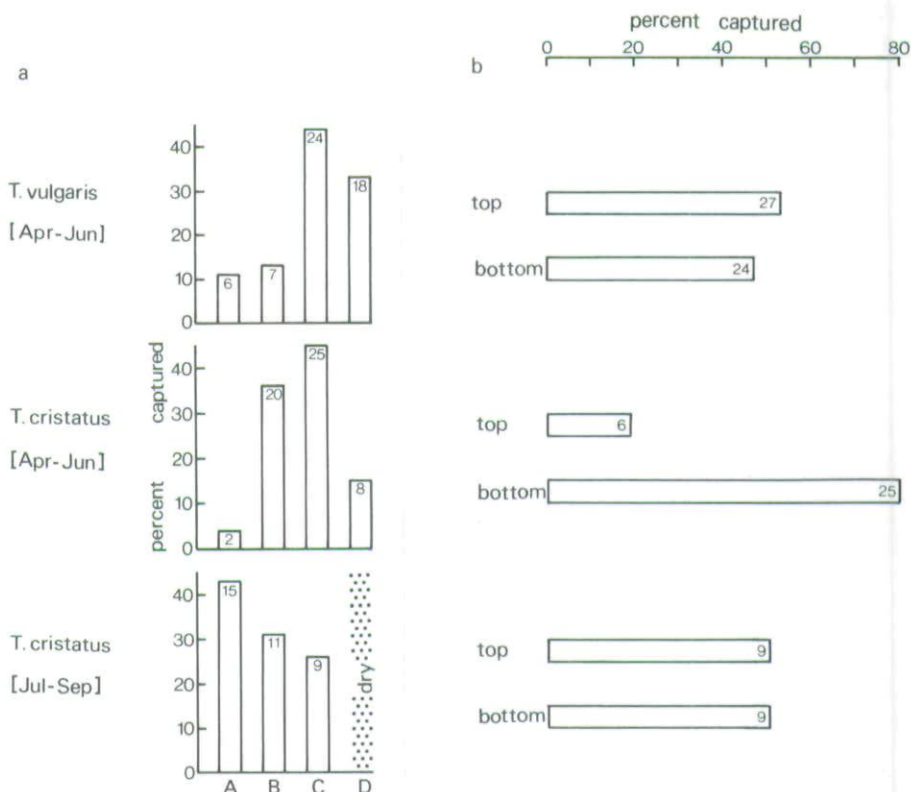
number of newts captured did not differ significantly between areas ($\chi_r^2 = 0.05$, $p > 0.05$). This trend of newts moving more towards the pond shoreline in July–September is further exemplified when the numbers captured in the north-west and south-east shorelines (areas E and F) are also taken into account. Of the total number of *T. cristatus* captured in the pond in April–June, 15% were found around the three pond shorelines. This compares with 60% being found in the same areas in July–September.

In terms of habitat selection within the water column, from April to June *T. vulgaris* showed no preference for the top or bottom of the pond in area C (Wilcoxon matched-pairs signed-ranks test, $T = 33.5$, $p > 0.05$), whereas significantly more *T. cristatus* were captured on the bottom than at the top ($T = 7$, $p < 0.01$). However, from July to September there was no difference between the top and bottom of the pond in the distribution of *T. cristatus* ($T = 18$, $p > 0.05$) (Fig. 3b).

Spatial niche overlap between *T. vulgaris* and *T. cristatus* in April–June was 0.640.

3.3. Feeding relations

A total of 44 *T. vulgaris* and 27 *T. cristatus* was stomach-flushed. Food items were obtained from 42 (95%) *T. vulgaris* and 25 (93%) *T. cristatus*, with 5% of *T. vulgaris* stomachs and 12% of *T. cristatus* stomachs also containing skin sloughs.

T. vulgaris stomachs contained a greater proportion of planktonic organisms than those of *T. cristatus* (Fig. 4). In terms of prey number, zooplankton (i.e. copepods, ostracods, and cladocerans) were the most abundant food items in the pond, and constituted 74% of the diet of *T. vulgaris*, compared with 36% in *T. cristatus*. This trend is emphasized by the volumetric analysis of prey items, which also demonstrates the overriding importance of leeches (*Erpobdella* spp.) in the diet of *T. cristatus*. Planktonic organisms constituted 29% of the diet by volume in *T. vulgaris*, compared with only 0.9% in *T. cristatus*. Leeches, however, accounted for 66% of the total volume of food items in *T. cristatus*, compared with 0.1% in *T. vulgaris*. The smaller organisms consumed by *T. cristatus*, however, were not significantly larger than those consumed by *T. vulgaris* (Tab. 1). Feeding niche overlap between *T. vulgaris* and *T. cristatus* was 0.621 (numerical analysis) and 0.243 (volumetric analysis). As the numerical analysis may overemphasize the importance of small prey taken in large numbers (Hyslop 1980), the volumetric analysis yields a more meaningful representation of the relative importance of different prey items in the diet.

Mayfly nymphs were abundant in the pond but constituted a relatively small proportion of the diet in both *T. vulgaris* and *T. cristatus*. Rather than indicating their apparent scarcity in the pond, the absence of leeches from the invertebrate samples probably reflects the ability of these organisms to escape netting by clinging to

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Fig. 4. Prey utilization by *T. vulgaris* and *T. cristatus* in relation to prey abundances in the pond: a, analysis by prey number; b, analysis by prey volume; l, larva; n, nymph; p, pupa; * prey categories found in stomachs but not in the pond.
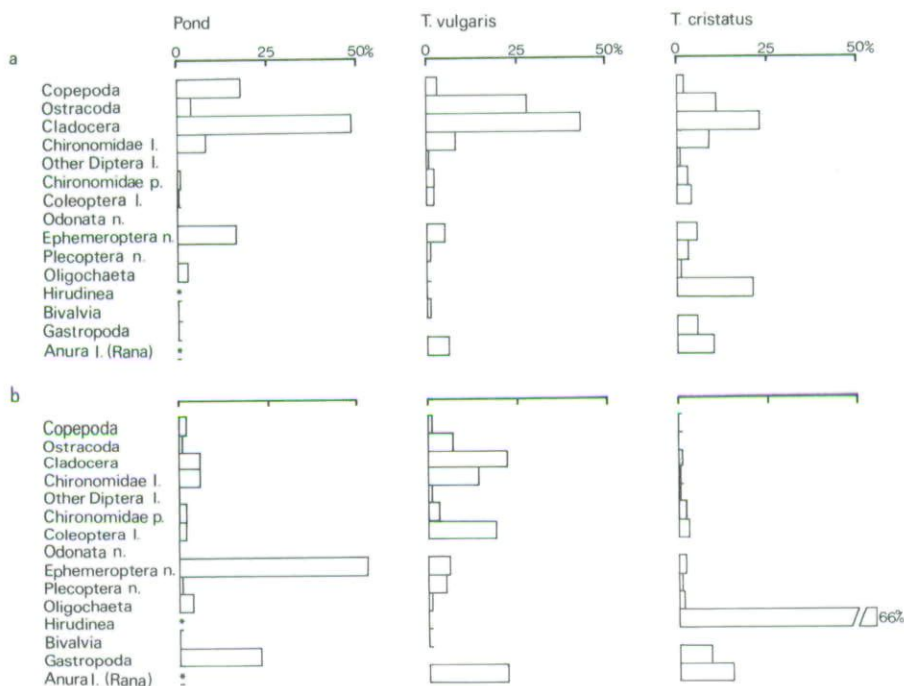
vegetation with the aid of their suckers. Moreover, visual inspection of the pond shorelines during the evening indicated that leeches were in fact moderately abundant. Likewise, frog tadpoles were not captured by netting because they were aggregated in one part of the pond only. The absence of leeches and tadpoles in the pond samples obviated the weighting of niche overlap indices by prey abundances, as has been conducted elsewhere (Griffiths 1986).

4. Discussion

Compared with the more evenly distributed *T. vulgaris*, *T. cristatus* was found mainly on the pond bottom in the central areas of Upper House pool during the first half of the summer. These results therefore confirm previous statements concerning differences between the two species in microhabitat selection (Cooke and Frazer 1976, Dolmen 1983b). However, the apparent change in microhabitat selection by *T. cristatus* in July–September is not easily explained. Such shifts during the course of the year could be interpreted in terms of the expansion

of the niche of one species in the absence of a competitively superior second species. This would imply that *T. vulgaris* in some way excludes *T. cristatus* from the surface and edges of the pond during April–June. However, as there may be changes in prey abundance and pond microclimate during the course of the year which may also influence habitat selection, the two periods are not directly comparable and such a conclusion is therefore tenuous. Behavioural and physiological changes during the course of the year may also affect habitat selection. By July the breeding periods of both species of newt are usually over (Smith 1969). The remaining summer months are therefore devoted to feeding, an activity carried out in water by *T. cristatus*, and on land by *T. vulgaris*. An unequivocal test of competitive exclusion can only be accomplished by experimentally excluding *T. vulgaris* from the pond and observing concomitant changes in microhabitat selection by *T. cristatus*.

As shown by previous studies (Avery 1968, Dolmen and Koksvik 1983), the dietary differences which exist between the two species appear to be a function of differences in body size. The present study demonstrates

Tab. 1. Comparison of sizes of small food items eaten by *T. vulgaris* and *T. cristatus*.

	n	*T. vulgaris* Median size (mm)	n	*T. cristatus* Median size (mm)	Mann-Whitney U	p
Ostracoda	30	1.2	10	1.2	166.5	>0.05
Cladocera	30	1.75	12	1.35	274	>0.01
Chironomidae larva	12	6.5	4	4.25	36.5	>0.05

that large size enables a wider range of prey sizes to be consumed, yet both large and small newts will consume small prey of similar size. In an experimental investigation of predation of tadpoles by newts, Cooke (1974) predicted that *T. cristatus* could consume tadpoles up to 50 mm in length, compared with a maximum size of 33 mm for *T. vulgaris*. Apart from such size differences, in Upper House pool both species of newts appear to be fairly unselective feeders, consuming different prey types approximately in proportion to their abundance. Such a foraging mode has also been observed in *T. vulgaris* and *T. helveticus* at another pond in mid-Wales (Griffiths 1986). In that they are generalist feeders, differing mainly in the sizes of prey consumed, newts conform to the pattern displayed by terrestrial salamanders (rev. by Toft 1985). Differences in diet between populations of the same species are therefore more likely to be a result of between-pond variations in prey availability than interpopulational differences in prey selection.

Feeding niche partitioning appears to be slightly more important than microhabitat niche partitioning in *T. vulgaris* and *T. cristatus*. In her extensive review of resource partitioning in reptiles and amphibians, Toft (1985) states that although food is commonly partitioned to some extent, habitat appears to be the dimension which is usually partitioned first. However, her review reflects a bias in the literature towards terrestrial salamanders, and the situation may be slightly different in aquatic newts. The mechanisms which bring about resource partitioning between *T. vulgaris* and *T. cristatus* are speculative. Size differences clearly may assist in reducing interspecific competition between the two species but whether competition resulted in selection for such character displacement in the first instance is less certain. Differences in body size may result from selection pressures which are independent of species interactions (Grant 1972). Large size may enable a species to gain a refuge from certain predators, and in turn, enable it to exploit predator-abundant microhabitats from which it was previously excluded. At many ponds the presence of fish may increase the potential of both competition and predation, and predatory fish may confine small species of newts to the shallow areas of ponds (Frazer 1978). Fish were absent from Upper House pool, although avian predators (notably herons) may have exerted some form of regulation on the newt populations. *T. cristastus* has been known to consume adult *T. vulgaris*, and the incidence of such predation may be high in certain populations (Hagström 1971, 1979). Indeed, Hagström (1979) suggests that under such predation pressure *T. vulgaris* may reduce the length of its aquatic period accordingly.

In assessing the causes of resource partitioning in newts, it is therefore clearly necessary to consider present-day interactions with heterospecifics and predators in the light of those selective pressures which may have resulted in differences in morphology.

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Appendix

Solids used to estimate prey volumes. Calculating formulae are shown at the bottom of each column. l, larva; n, nymph; p, pupa.

Cylinder	Elliptical cylinder	Hemi-ellipsoid	Oblate spheroid (ellipsoid)	Prolate spheroid (ellipsoid)
Chironomidae l.	Hirudinea	Copepoda	Cladocera	Ostracoda
Chironomidae p.			Bivalvia	Gastropoda
Other Diptera l.				Anura l.
Coleoptera l.				
Odonata n.				
Ephemeroptera n.				
Plecoptera n.				
Oligochaeta				
$2a(\pi b^2)$	$2a(\pi bc)$	$0.5(4\pi ab^2/3)$	$4\pi a^2b/3$	$4\pi ab^2/3$
Length = 2a, width = 2b, depth = c				