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ON THE DISTRIBUTION OF THE PALAEARCTIC NEWTS (GENUS *TRITURUS)* INCLUDING THE DESCRIPTION OF A FIVE SPECIES POND IN WESTERN FRANCE

J. W. ARNTZEN and P. DE WIJER

Institute of Taxonomic Zoology, University of Amsterdam, Mauritskade 57, P.O. Box 4766, 1009 AT AMSTERDAM, THE NETHERLANDS

INTRODUCTION

Since the publication of Thorn's (1968) excellent handbook on the biology of the Palaearctic salamandrids twenty years ago, a large amount of data has accumulated in the literature. Most attention has been given to those species that have their distribution in western Europe. The knowledge of *Triturus*, the genus of Palaearctic aquatic salamanders, has especially profited from the increased interest in amphibian biology. Ecological studies by our collegues and ourselves on the amphibians of western France and the updated distribution maps presented by Macgregor, Sessions and Arntzen (1989) provide the focus for the present observations. The paper is in two parts. The first part concentrates on the distribution and ecology of five species of newts in the département (province) of Mayenne in western France. In the second part we relate our observations to the overall distribution patterns in *Triturus* and try to provide an explanation for the high number of species that can be found in France.

SYMPATRY OF FIVE SPECIES IN FRANCE

The approximate boundaries of the ranges of the five species of *Triturus* found in France are shown in Fig. 1. *T. helveticus* is the most widespread and can be found all over the country, with the exception of the alpine region in the southeastern part. *T. alpestris, T. cristatus* and *T. vulgaris* are distributed over the northern and central parts of France. The southernmost occurrences of these three species are recorded in the east; in western France *T. vulgaris* has a wider distribution than the other two species. The distribution of *T. marmoratus* is restricted to the central and southern parts of the country. The area in which all five above-mentioned species show range overlap is a relatively narrow zone in central France. Towards the west the zone is wider than in the east. This zone accommodates the maximum number of *Triturus* species (five) to be found sympatrically. Indeed, the presence of the five species was reported from the vicinity of Rennes (Abbayes, 1932).

In 1979 an inventory was made by J. Schoorl and A. Zuiderwijk in the département Mayenne which is located in the centre of the widest part of the zone of sympatry. Their records and additional data have been presented by Evrard and Daum (1982) in a grid system with rectangular areas ('squares') of approximately 7 x 10 km. This grid system is based on the French topographical maps of the Institute Géographique National. The maps of scale 1/50,000 cover eight squares.

Three major landscape types can be recognized in Mayenne (Fig. 2). The northern part is hilly and forested, the southern part is flat and open, and the central part is flat and forested. This latter landscape type, the so-called 'watery area' of Schoorl and Zuiderwijk (1981), is characterized by a hydromorphic soil and many ponds can be found in this area. Although the inventory of Schoorl and Zuiderwijk comprised the whole département and over 300 sites were investigated, a pond accommodating all five newt species was not documented. *T. helveticus* is widely distributed all over the département and recorded from all three landscape types. In Mayenne, *T. helveticus* is the most abundant amphibian species (Schoorl and Zuiderwijk, 1981), recorded in 55 squares. When the squares that are located partially outside Mayenne are omitted from the analysis, the species occurs in 46 out of a total of 57. Accordingly, the index of presence *(P)* of the species can be computed at (46/57) x 100% = 81%.

T. alpestris and *T. vulgaris* are the rarest newt species in Mayenne (Schoorl and Zuiderwijk, 1981), with *P* values of 19% and 14% respectively. *T. alpestris* is found in the southwestern

Figure 1. The distribution of the genus *Triturus* in France (after Macgregor, Sessions and Arntzen, 1989). Indicated are the approximate range borders of : *T. cristatus* (open round symbols), *T. marmoratus* (solid round symbols), *T. alpestris* (triangle symbols), *T. helveticus* (open square symbols) and *T. vulgaris* (sold square symbols). Symbols are placed at the inner side of the species' ranges. In black : the département Mayenne.

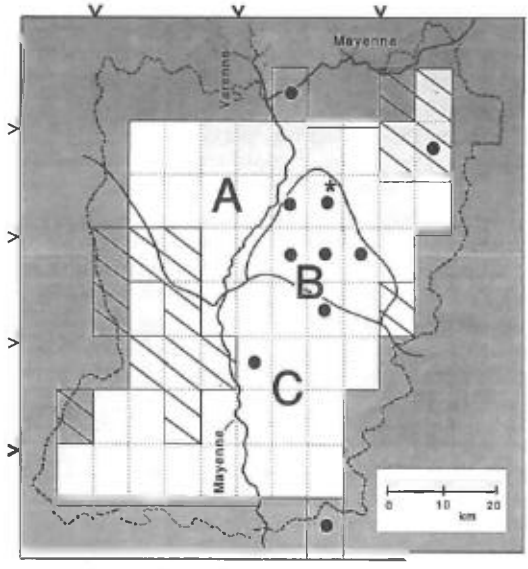

Figure 2. Schematic representation of the distribution of newts in dept. Mayenne, France, according to Schoorl and Zuiderwijk (1981), Evrard and Daum (1982) and observations of the authors. *T. cristatus* is found in area B, C and sporadically in A, *T. marmoratus* is found in area A, B and occasionally in C. *T. alpestris* is found in the hatched 'squares'. *T. vulgaris* is widespread in area B and found occasionally in area A and C (squares indicated by solid round symbols). *T. helveticus* is found in most squares all over the département (light shading); records from squares (partially) outside Mayenne are ignored. The location of the newly described five species pond is indicated by an asterisk. Landscape types are: A - hilly area, B - pond rich area with hydromorphic soil, C - flat area, according to Schoorl and Zuiderwijk (1981). The dark shaded squares are the ones located (partially) outside the département Mayenne. Arrows at the edge of the map refer to the formats of the topographical maps of scale 1/50,000.

and the northeastern corners of the département and at the southeastern corner of the hydromorphic soil area. *T. vulgaris* is recorded from ten squares in the east of the département; as yet no populations of *T. vulgaris* have been found west of the rivers Varenne and Mayenne (Fig. 2). Most records come from the area with hydromorphic soil. The more detailed inventory that we performed in that area indicates that the species may well have a wider distribution than is documented. We found it in 35 out of 91 ponds investigated, but often in low frequencies. Large samples of newts are generally required to demonstrate its presence. In six ponds only *T. vulgaris* was more abundant than *T. helveticus.*

The two large bodied species, *T. cristatus* and *T. marmoratus,* for which *P* is 56% and 46% respectively, are widely distributed. *T. marmoratus* is distributed in hilly and forested areas in the northern parts of Mayenne and occasionally in the south, while *T. cristatus* is abundant in the flat areas in the south of the département and found sporadically in the north. Detailed field studies indicate that these species generally have mutually exclusive, parapatric rather than sympatric distributions (Zuiderwijk, 1980; Schoorl and Zuiderwijk, 1981). The area with hydromorphic soil in the centre of Mayenne is exceptional as it accommodates both species, often coexisting in the same pond (Arntzen, 1986).

Assuming a random distribution of newts over the département and a random inventory, the probability of finding a square with all five species can be calculated by multiplication of the recorded *P* values. The result predicts a small chance (approximately 0.6%) of recording five species in a single square. The relative scarcity of some species of *Triturus* in Mayenne, combined with the parapatric distribution pattern of others led us to believe that four was the maximum number of species to co-exist in a pond. All the greater, then, was our surprise when one of us (PdW) demonstrated the occurrence of *T. alpestris* in a pond at the edge of the hydromorphic soil area, where the other four species were also found.

The pond is situated 1 km north of the hamlet of Grazay (Fig. 2) in a small piece of wood surrounded by meadows. The site is a former quarry of manganese. The quarry was created early in the 19th century and in use till 1840. Later on it served as a refuse dump. When the dump was covered up, the size of the pond was substantially reduced (B. Cheminau, pers. comm.). The main feature of the pond is its heterogeneity (Fig. 3). It has a large irregular surface area of approximately 1500 m^2, with shallow – deep (2.5 m), shaded – sunny and vegetated – nonvegetated parts. In early spring, parts of the surrounding woods are flooded. In exceptionally dry years it may dry up completely but generally the pond is permanent. Dominating plant species in the pond are *Lemna* sp., *Hottonia palustris, Ranunculus* sp., *Iris pseudacorus, Oenanthe aquatica* and the algae *Cladophora* sp. Due to forestry work many trunks and branches are laying in the water. Three visits to this pond during the reproductive season of the newts in 1987 gave the following catching results: 2 *T. cristatus,* 2 *T. marmoratus,* 6 *T. vulgaris,* 15 *T. helveticus* and 53 *T. alpestris.* During a visit in early April 1989 again the five species were found (1 *T. cristatus,* 3 *T. marmoratus,* 3 *T. helveticus,* 9 *T. vulgaris* and 17 *T. alpestris).* All males were in breeding condition and the females were spawning. To the best of our knowledge this is the first record of a pond that accommodates five species of *Triturus.*

In Mayenne, a number of ponds with four species have been recorded and more often than not *T. alpestris* is the missing species. The distribution pattern of *T. alpestris* all over Europe indicates that it is a mountain dwelling species. This is particularly clear at the southern edges of its range where relict populations are found in mountainous regions. Also, it is a newt that is more often found in shaded ponds than any of the other species. In Mayenne, however, a preference of *T. alpestris* for the northern hilly area is not evident, nor is *T. alpestris* recorded from any of the large forests. As yet we do not know how to explain its fragmented distribution in this area.

DISTRIBUTION OF THE GENUS *TRITURUS*

Newts of the genus *Triturus* are found in all European countries with the exception of Iceland and Malta. Some species occur in adjacent parts of Asia, such as Turkey, Iran, Syria, Lebanon and Israel. Fig. 4 is a somewhat simplified map representing the co-occurence of species, based on the updated distribution maps for all twelve *Triturus* species by Macgregor, Sessions and Arntzen (1989). It demonstrates that newts are absent in the colder areas of northern Europe

Figure 3. Pond accommodating five species of *Triturus*.

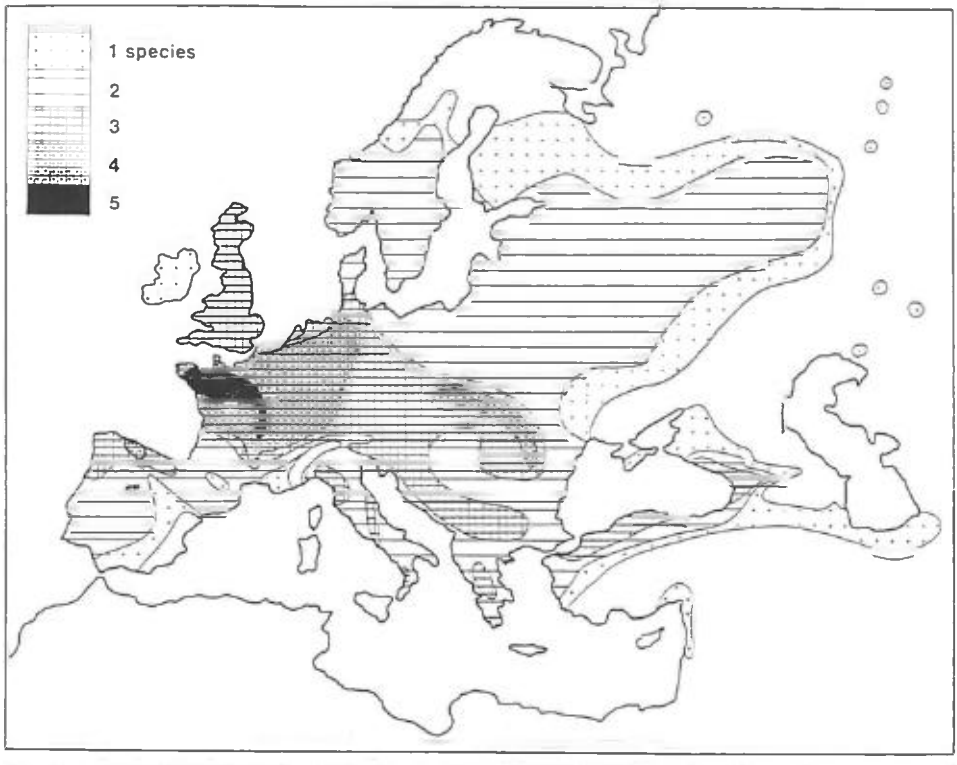

Figure 4. Species density contour map for the genus *Triturus* (simplified after Macgregor, Sessions and Arntzen, 1989).

and in the drier areas of the southern USSR and the Middle East. The highest rate of species density is found in western Europe. In our opinion two factors are influencing this pattern of species distribution, a climatological and a historical one.

High levels of annual rainfall are found in the subatlantic region. The rainfall pattern clearly coincides positively with the species density distribution of *Triturus*. This interpretation of the distributional and pluviometric maps is enforced by the fact that a relatively high number of species (three) is found to the south and east of the Black Sea, an area characterized by high precipitation (Schmidtler and Schmidtler, 1967). Precipitation appears to be an important factor in the distribution of newts. An exception to the general pattern is found in the upper regions of the Pyrenean Mts. and at the southern fringes of the Alps. Most secondary mountain ranges have relatively high rates of species density. A major component of this pattern is the distribution of two mountain dwelling species: *T. montandoni,* a species endemic to the Oder and Carpathian Mts., and *T. alpestris*. For North America, Kiestler (1971) concludes that species diversity of the Amphibia is positively correlated with secondary mountain regions and with annual rainfall. We conclude that the main parameters influencing species diversity of Palaearctic newts are the same as those for the amphibians of the Nearctic.

Secondly, we have to consider the biogeographical history of the newts in the light of the Pleistocene climatological events known as the Ice Ages. The harsh climatic conditions in the northern parts of Europe made life impossible for newts. Refuges during the last Ice Age can be hypothesized in a straightforward way from the present-day distribution of the species (Zuiderwijk, 1980; Wilkinson, 1988). The southern European peninsulae (Iberian, Apennine, and Balkan Peninsula) are likely pleniglacial refuges for newts as well as for many other plant and animal species, while the refuge of *T. montandoni* may have been situated in the southern part of the Carpathian mountains. When the climatic conditions improved at the end of the Weichselian, about 12,000 BP, the species were able to recolonise central and northern Europe. Some species, but not all, reached the British Isles before they became separated from continental Europe by the rising sea level (see Wilkinson, 1988, and references therein).

The actual distribution pattern of newts and that of European amphibians in general, indicates that the postglacial invasion of northern Europe was most successful from the southwestern (Iberian Peninsula) and the southeastern (Balkan Peninsula) refuges. Few species found a refuge in the Apennine Peninsula, probably because it is more isolated from the rest of Europe (by the arc formed by the Alps) than the other peninsulae are (Zuiderwijk, 1980; 1984). Zones of postglacial secondary contact are found all over Europe and well documented examples exist for various animal groups (Hewitt, 1988). In species that frequently or occasionally hybridize most of these zones seem to be narrow. Parapatric distributions are found more frequently than widely overlapping distributions. In the genus *Triturus* many such zones of secondary contact have been found, for example in southeastern Europe where the four members of the *Triturus cristatus* superspecies show an essentially parapatric type of distribution (Wall and Arntzen, 1989; Macgregor, Sessions and Arntzen, 1989). Another narrow contact zone, between *T. montandoni* and *T. vulgaris,* may exist in the foothills of the Carpathian Mountains, but their distributions in relation to one another are not yet precisely documented.

Highest species density is often taken as an indication for the centre of dispersal. In newts this would point to western France, but we feel that this notion is misleading. We have to consider the origin and radiation of *Triturus,* and separate it from the present-day climatologically induced distribution patterns and routes of postglacial dispersal. Morphological and genetic variation within *Triturus* species is highest in southeastern Europe and adjact Asia (Schmidtler and Schmidtler, 1983; Kalezic, 1984; Arano and Arntzen, 1987). Species diversity likewise is the highest in this area although many species are not distributed sympatrically. In southern Europe five (sub)species occur on the Iberian Peninsula, four on the Apennine Peninsula while six (sub)species are found in the Asiatic part of Turkey and ten in the Balkan Peninsula (Macgregory, Sessions and Arntzen, 1989). In our opinion, this is evidence that the Balkan Peninsula, rather than western Europe, is the centre of dispersal of *Triturus.*

The taxonomic relationships within the family Salamandridae are not resolved unequivocally and it is not clear which genera are phylogenetically closest to *Triturus.* The available evidence suggests a close relationship of *Triturus* to the genera *Neurergus* and *Paramesotriton* (Wake

and Özeti, 1969). These genera have Central Eastern and Far Eastern distributions, respectively, which points to an eastern Palaearctic origin for this group of Salamandrid genera as a whole. This again would better fit the view that the Balkans is the centre of dispersal for *Triturus*, rather than western Europe.

So we conclude that the present-day high rate of species density in western France is of postglacial origin, does not reflect the centre of dispersal of the genus *Triturus* and is in line with climatological patterns. Up to five *Triturus* species may occur in sympatry and, in exceptional cases, share breeding sites. This situation, as found in western France, provides unique opportunities to study the interspecific ecological relationships of newts. Comparisons may involve closely related species, *T. helveticus* – *T. vulgaris* and *T. cristatus* – *T. marmoratus*, as well as more distantly related species, for example all comparisons involving *T. alpestris*.

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