

AMPHIBIAN DISTRIBUTION PATTERNS IN WESTERN EUROPE

by

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ABSTRACT

Mechanisms controlling the distribution of amphibians in western Europe have been studied in France where related species, isolated from each other at least during the last glacial period, are now sympatric.

Occurrences and biotope preferences of the various species were investigated in several regions, with attention to the position of each region within the ranges of the species: central or peripheral. For some species the previously known distribution boundary is partially precised.

The population densities of related species in their zones of overlap are discussed. Three pairs of species are considered in particular. *Triturus helveticus* and *T. vulgaris* have a large sympatric area in which they appear to be gradually replacing one another. Competition is considered to be unimportant, the distribution boundary of *T. vulgaris* in central France is determined primarily by climatological factors, causing typically a vague border. *Rana temporaria* and *R. dalmatina* occur largely sympatric. Very little can be found suggestive of mutual influences. The intensity of occurrence of *R. temporaria* and the preference of habitats seem to be dependent upon local climatological circumstances. The closely related *Triturus cristatus* and *T. marmoratus* both appear to be common in a relatively narrow zone. Within this zone the species occupy rather distinct biotopes, presumably due to ecological displacement. In this case the distribution boundaries are sharp.

Phenomena connected to relationship are considered for pairs of species of Europe.

I. INTRODUCTION

The purpose of the present investigation is to trace the circumstances influencing occurrence and distribution of amphibians in Europe west of the Alps.

In this context it has proved useful to study a species in various regions within its range. Both the centre of the area, where in general the species is common in many different biotopes, as well as the marginal reaches, where the species is often more choisy, are important in this respect. Our investigations are focussed on the comparison of central and marginal biotopes, based on which it is attempted to elucidate the nature of the distribution boundary. This boundary is dependent upon limiting factors, which may be of biotic or abiotic nature. In the present study we are dealing mainly with the influence of climate, soil and several biotic factors. The present distribution of the species however, is the result of expansion from their refuges after the last ice age.

During the last Pleistocene ice age (Würm, 90,000-10,000 years B.P.) the species to be discussed occupied one or more separate or non-separate refuges, viz. the Iberian peninsula and the Balkan peninsula with the steppes along the Black Sea and the Caspian Sea, called the western refuge and the eastern refuge, respectively, in the following. Most populations of the Italian peninsula refuge could not expand northwards because of the immense barrier presented by the Alps. In table I the species and the refuges they probably occupied are given.

When the climate ameliorated the species spread over Europe. These expansions were influenced by obstacles, geographical barriers, like the Alps and in a lesser degree (because of corridors on both

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TABLE I

Ice age refugia of western European amphibians.

Refuge during Würm	Actual distribution and northernmost records	Species
WESTERN REFUGE	restricted to the Iberian peninsula	<i>Chioglossa lusitanica</i> Bocage, 1864
	ibid.	<i>Triturus boscai</i> (Lataste, 1879)
	ibid.	<i>Alytes cisternasii</i> Boscá, 1879
	ibid.	<i>Rana iberica</i> Boulenger, 1879
	ibid.	<i>Pleurodeles waltl</i> Michahelles, 1830
	Pyrenees	<i>Euproctus asper</i> (Dugès, 1852)
	relict populations on the Iberian peninsula	<i>Hyla arborea</i> Linnaeus, 1758
	ibid.	<i>Triturus alpestris</i> (Laurenti, 1768)
	southern France	<i>Discoglossus pictus</i> Otth, 1837
	up to central France	<i>Pelobates cultripes</i> (Cuvier, 1829)
	ibid.	<i>Hyla meridionalis</i> Boettger, 1874
	ibid.	<i>Triturus marmoratus</i> (Latreille, 1800)
	ibid.	<i>Rana esculenta</i> complex *)
	northern France	<i>Pelodytes punctatus</i> (Daudin, 1803)
	southern part of The Netherlands and part of the G.F.R.	<i>Alytes obstetricans</i> (Laurenti, 1768)
ibid.	<i>Salamandra salamandra</i> (Linnaeus, 1758)	
ibid.	<i>Triturus helveticus</i> (Razoumowski, 1789)	
southern Scandinavia	<i>Bufo calamita</i> Laurenti, 1768	
SOUTHERN EUROPE	up to and including northern Scandinavia	<i>Bufo bufo</i> (Linnaeus, 1758)
	ibid.	<i>Rana temporaria</i> Linnaeus, 1758
EASTERN REFUGE (possibly including Italy)	all Sweden and Finland	<i>Rana arvalis</i> Nilsson, 1842
	central Scandinavia	<i>Triturus cristatus</i> (Laurenti, 1768)
	ibid.	<i>Triturus vulgaris</i> (Linnaeus, 1758)
	southern Scandinavia	<i>Bombina bombina</i> (Linnaeus, 1761)
	ibid.	<i>Bufo viridis</i> Laurenti, 1768
	ibid.	<i>Rana esculenta</i> complex *)
	ibid.	<i>Hyla arborea</i> Linnaeus, 1758
	ibid.	<i>Pelobates fuscus</i> (Laurenti, 1768)
	Denmark	<i>Triturus alpestris</i> (Laurenti, 1768)
	southern Scandinavia (relicts)	<i>Rana dalmatina</i> Bonaparte, 1840
	northern G.F.R.	<i>Salamandra salamandra</i> (Linnaeus, 1758)
	ibid.	<i>Bombina variegata</i> (Linnaeus, 1758)

We made "a sophisticated guess" of the most probable refuges for the species with respect to the geographical extent of the present ranges (according to Thorn, 1968, Arnold & Burton, 1978, and others). In the table the species are divided according to their probable refuges, an eastern and a western refuge. Southern Europe is added to indicate the possibility that the ranges of some species remained in contact north of the Pyrenees, Alps, etc. Italy is not represented as a separate refuge in the table because hardly any species expanded from there into the part of western Europe studied here; two species though might have done so, *Rana lessonae* and *Rana dalmatina*. However, recent finds of possibly *R. lessonae* near the Black Sea (Hotz, 1974) suggest a large distribution area during the Würm for this species. With regard to *R. dalmatina* it is not clear whether an Italian or a Balkan population has been responsible for occurrence of the species in France and northern Spain nowadays.

From the western distribution centre ten species came north of the Pyrenees and nine of them occur in one or more of the areas under study here, some of which at their northern limit.

The species of the eastern distribution centre that are restricted to eastern Europe have been omitted from the table. The tabulated species, however, spread out far to the north. Ten of them occur in the presently investigated part of western Europe, most of them at their southern limit.

*) The *Rana esculenta* complex consists of *Rana ridibunda* Pallas, 1771, *Rana lessonae* Camerano, 1891, and their hybrid "*Rana esculenta*" Linnaeus, 1758. *R. ridibunda* occupied the Iberian peninsula and the Balkan area, *R. lessonae* occurred at least in Italy. The actual northern boundaries of both species and of "*R. esculenta*" follow approximately the same line.

sides), the Pyrenees. Also minor topographical features, such as the river Loire, have influenced the distribution of at least one species, *Triturus alpestris*. The regions presently under study are located in France, in a zone where species having expanded from the eastern refuges and those from the western refuge occur sympatric. In this way we find areas of sympatric occurrence for the following pairs of species: *Triturus cristatus* and *Triturus marmoratus*, *Triturus vulgaris* and *Triturus helveticus*, *Hyla arborea* and *Hyla meridio-*

nalis, *Rana dalmatina* and *Rana temporaria* and, probably, *Pelobates fuscus* and *Pelobates cultripipes*. Attention is paid here notably to interaction between related species in sympatric areas.

II. REGIONS INVESTIGATED AND METHODS

We investigated the following regions because of their strategic location: the region north of Boulogne-sur-Mer in northwest France, the Sancerre region (and adjacent areas) in central France, the

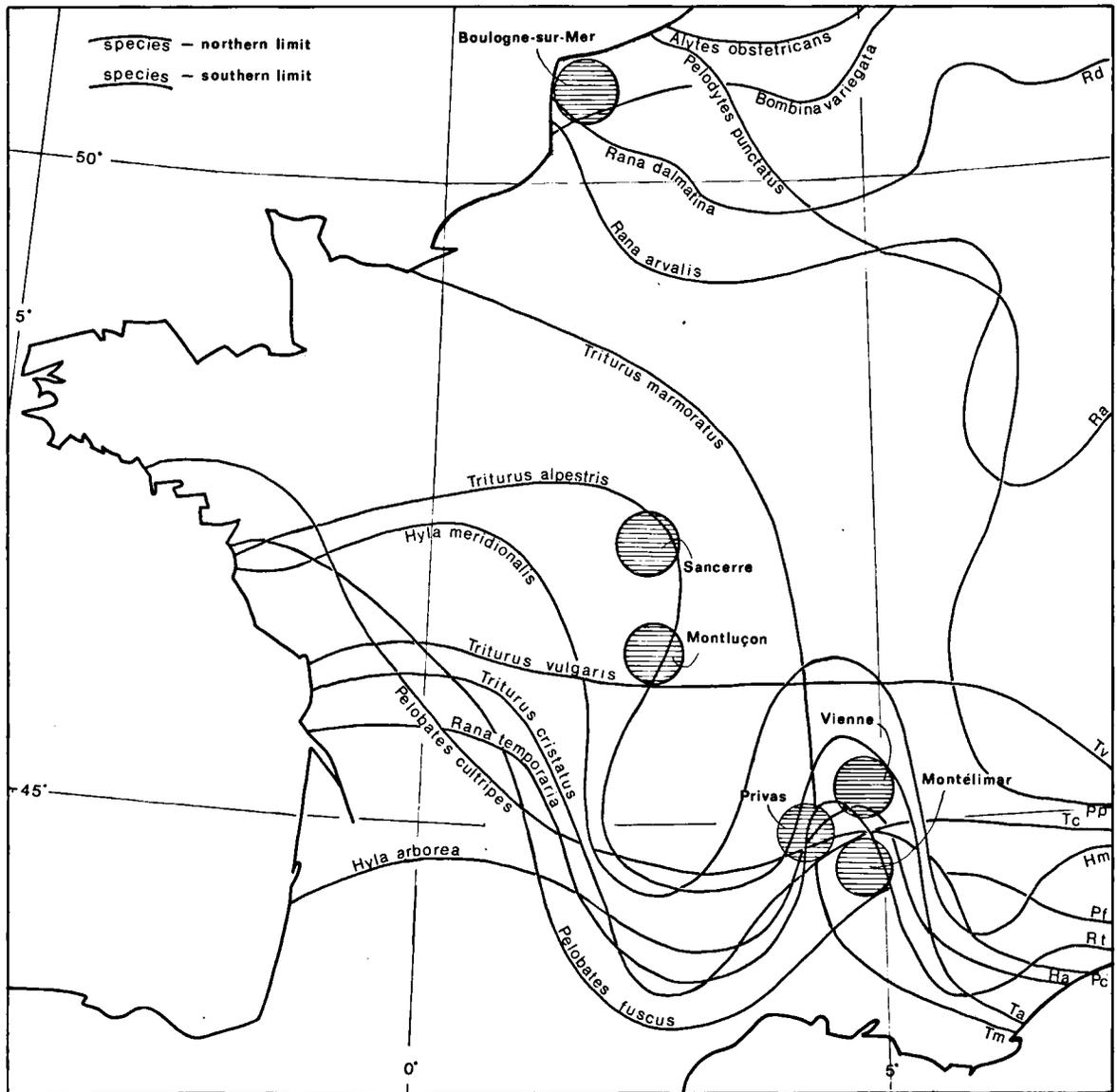


Fig. 1. Location of the areas investigated and distribution boundaries of amphibians in France after Arnold & Burton (1978). Difference is made between northern and southern boundaries by placing the species name inside its range.

Montluçon region in central France at the north-western foot of the Plateau Central, the regions of Vienne and Montélimar in the Rhône Valley with an adjacent area (Privas) on the Plateau Central. Fig. 1 shows the location of the investigated regions together with the amphibian distribution boundaries, according to Arnold & Burton (1978).

The Boulogne-sur-Mer region (départ. Pas-de-Calais) is situated around the mouth of the small river Slack, on the French Channel coast. The scenery shows hills in limestone, marl, shale and sandstone, river plains and swamps, and dunes and cliffs at the coast. The hilly terrain is used predominantly as pasture ground and less for arable farming. Limestone quarries are found locally. Much surface water is found in this variegated area yielding a great variety of breeding biotopes for amphibians: swamps along river and brooks, marshy depressions in the dunes, abandoned inundated quarries, ponds at springs, and cattle watering pools.

Sancerre (départ. Cher) lies along the Loire. The investigated region may be divided in: (1) the north-south running Loire valley, a river plain, 1 km wide at most, underlain by gravel, sand, clay and peat, where swamps, pastures and fields are found; (2) a gently undulating terrain west of the Loire valley with occasional steeper slopes where viticulture is carried out; other slopes of the hilly terrain, cut by numerous brooks, are used for cattle-breeding and agriculture; (3) the most western strip of the area, which is wooded. Much stagnant surface water is found in the region: swamps along rivers and brooks, marshy spots in the woods on the plateaus, lakes everywhere in valleys, ponds at springs and watering pools. The larger reservoirs are unfit for most amphibian species because of their large dimensions and, notably, because they are stocked with fish. Adjacent areas inventoried are: Lorris, Clamecy, Parc du Morvan and Bourbon.

The Montluçon region (départ. Allier) is situated at the foot of the Plateau Central. It represents a transitional region between the mountainous Plateau Central and the lower, hilly area of central France. Along the rivers Cher and Allier we find alluvial plain deposits like along the Loire. The

rest of the area is underlain by a great variety of rock types; limestone is scarce, however. The soil is poor in general. Pastures alternate with forests and agriculture is unimportant. Water seeps out of the slopes on a strikingly great number of places. The springs often serve as watering place for cattle and they make very suitable breeding sites for amphibians. Apart from these pools there are larger and smaller lakes and marshy pools in the forests.

The Vienne region is situated in southeastern France at the border of the départements Drôme and Isère, 80 km south of Lyon and 25 km east of the Rhône. The area is underlain mainly by gravel and sand. Some plateau-topped east-west running ridges are conspicuous in this region, causing a division of the landscape in plateaus under forests (oak and birch) on poor soils, slopes with forests and pastures and plains in the valleys with fields. Stagnant surface water is restricted to lakes and shallow pools and puddles on the poorly drained plateaus, smaller lakes and springs on the slopes and ditches in the valley plains. The ponds at springs and the smaller lakes without fish are especially important as breeding sites for amphibians, the shallow pools and puddles, such as cart tracks, are poor in species.

The Montélimar region (départ. Drôme) is situated a 100 km south of the Vienne region. It is a flat sandy terrain between the Alps and the Rhône River. We find a few ponds at springs, furthermore amphibian breeding sites are restricted to the large riverbeds where in summer shallow puddles become isolated from the watercourse and serve as breeding places, especially for toads.

The Privas region is the small eastern fringe of the Plateau Central from Montélimar up to Vienne.

METHODS

Of the investigated areas, viz.: Boulogne-sur-Mer, Sancerre, Vienne, Montélimar, Privas and Montluçon, the first four have been investigated quite thoroughly, the others only occasionally. In the intensively searched regions, investigation started in the beginning of March and was continued till in July, during which period the potential spawning sites were mapped. The particulars of the biotopes were described and the amphibian species enumerated. The sites were visited several times during the season and nocturnal visits, especially during the breeding seasons, completed the inventory. Besides

the intensive inventory of the regions in question, incidental inventories were made in adjacent areas.

For the description of the spawning sites attention was paid to (1) factors concerning the landscape, viz.: nature of the soil and bedrock, topography, land use; (2) factors concerning the reproduction site, viz.: dimension, depth, nature of the banks, sunshine, water quality, water vegetation, presence of food, predators and competitors.

As many quantitative data as possible were checked; relative data, like numbers of adults and egg masses actually seen, were completed occasionally with more absolute numbers, estimated by means of applying a method of capturing-marking-recapturing. As the pools of the intensively examined regions have been visited several times, we assume that we have succeeded in making an inventory of practically all species of amphibians occurring there.

The inventories have been made by: Arntzen, Gerats, Hooghiemstra & Zuiderwijk for the Boulogne-sur-Mer region in 1974-1975; Zuiderwijk for the Sancerre region in 1977; Schoorl & Zuiderwijk for the Montluçon region in 1978; Zuiderwijk for the Vienne, Montélimar and Privas regions in 1978.

III. RESULTS

1. Review of all inventories

A review of the inventories of all regions is listed in table II. Habitat preferences will be mentioned later for every region apart.

Table II shows the location of the regions with respect to the ranges of the species concerned (central or peripheral), the population densities we encountered there and also whether a species is expected there according to literature.

Some species appear to be rare in all the regions, viz.: *Bombina variegata*, both *Pelobates* species, *Pelodytes punctatus*, both *Hyla* species and *Rana arvalis*. Other species may be found in abundance, e.g. *Rana dalmatina* in central and southeastern France, *Rana temporaria* in the northern regions. The same applies to the *Triturus* species, *vulgaris* and *helveticus*: *T. helveticus* is very common almost everywhere in France, which is true for *T. vulgaris* in the northern regions only. These instances illustrate that, as a rule, the population density within the range is often greater in the central parts than near the boundaries.

2. The various regions and habitat preferences

2.1. The Boulogne-sur-Mer region. — In table II we see the expected (according to literature) and the actually observed species. Among the amphib-

ians to be expected, only *Pelobates fuscus* was not found, and, after 5 years investigation of the Boulogne-sur-Mer region, we may say that the species is not likely to occur there.

The observed distribution of amphibians in various elements of the landscape is shown in table III.

The four *Triturus* species are common to abundant. *T. helveticus* and *T. vulgaris* are common in all elements of the landscape and *T. cristatus* and *T. alpestris* are found in ponds and pools and in abandoned quarries in hilly country together with *T. helveticus* and *T. vulgaris*.

Alytes obstetricans accompanies the *Triturus* group. We have not found the Midwife Toad along brooks and in the valley of the river Slack. The swamps, notably along the river Slack, provide an important habitat to *Rana temporaria* and *Bufo bufo*. In addition, many toads also mated in forest pools.

The coastal dunes represent an important area for all species except for *Salamandra salamandra* and *Triturus helveticus*.

"*Rana esculenta*" is common in the swamps near the town of Guines, 40 km inland, but appears to be rare in the surroundings of Boulogne-sur-Mer, as is *Rana arvalis*. The latter species, however, approaches its southern boundary here.

The presence of *Pelodytes punctatus* near Sangatte (Kroese & Van Leeuwen, 1979) represents the northernmost occurrence of this species known at present.

The Boulogne-sur-Mer region is exceptional since many species are found in great numbers at many sites and also because many species mate in the same water body, up to ten different species in one pool. The group of species discussed here shows interspecific predation in those pools, to such a degree that the entire offspring of certain species is eaten.

2.2. Sancerre and adjacent regions. — The location of the areas investigated is shown in fig. 2. The distribution of the amphibians in the various elements of the landscape at Sancerre is shown in table IV, part A.

In this region *Triturus helveticus*, *Rana dalmatina* and *Rana esculenta* complex (see fig. 5 for

TABLE II
Distribution of amphibians in the investigated regions.

	← north				south →			
	Maastricht ** n = 230	Boulogne-sur-Mer n = 213	Sancerre and adjacent regions n = 181	Montluçon n = 140	Vienne n = 198	Montélimar n = 40	Privas n = 39	
<i>Salamandra salamandra</i>	▨ +p	▨ +p	▨ +c	▨ +c	▨ +c	▨ +c	▨ +c	▨ +c
<i>Triturus marmoratus</i>	-	-	□ +p	▨ +p	-	-	?	
<i>Triturus cristatus</i>	▨ +c	▨ +c	▨ +p	▨ +p	□ +p	-	▨ +p	
<i>Triturus alpestris</i>	▨ +c	▨ +p	□ -	▨ +p	▨ +p	-	□ +p	
<i>Triturus vulgaris</i>	▨ +c	▨ +c	□ +p	□ +p	-	-	?	
<i>Triturus helveticus</i>	▨ +p	▨ +c	▨ +c	▨ +c	▨ +c	▨ +c	▨ +c	
<i>Bombina variegata</i>	□ +p	-	□ +c	▨ +c	▨ +p	+p	▨ +c	
<i>Alytes obstetricans</i>	▨ +p	▨ +p	▨ +c	▨ +c	▨ +p	▨ +p	▨ +c	
<i>Pelobates cultripes</i>	-	-	-	-	-	▨ -	-	
<i>Pelobates fuscus</i>	□ +p	+p	+p	+p	+p	-	+p	
<i>Pelodytes punctatus</i>	-	▨ +p	□ +c	+c	+c	▨ +c	+c	
<i>Bufo bufo</i>	▨ +c	▨ +c	▨ +c	▨ +c	▨ +c	▨ +c	▨ +c	
<i>Bufo calamita</i>	▨ +c	▨ +p	□ +c	+c	+p	▨ +p	□ +p	
<i>Hyla arborea</i>	□ +c	▨ +p	▨ +c	▨ +p	+p	▨ -	+p	
<i>Hyla meridionalis</i>	-	-	-	□ -	+p	□ +p	-	
<i>Rana temporaria</i>	▨ +c	▨ +c	▨ +p	▨ +p	▨ +p	-	□ +p	
<i>Rana arvalis</i>	□ +c	□ +p	-	-	-	-	-	
<i>Rana dalmatina</i>	-	-	▨ +c	▨ +c	▨ +c	+p	+c	
<i>Rana esculenta</i> complex	▨ +c	□ +p	▨ +c	▨ +c	▨ +c	▨ +c	▨ +c	

The regions are arranged in a north-south order, except Privas (Plateau Central) because of its deviating altitude.

n = Number of pools investigated.

The encountered population densities are given by squares, viz.: open, hatched, blocked and black which means, resp.: the species was observed in 5% of the investigated pools at maximum, in 5 to 15%, in 15 to 40%, over 40%.

The expectation whether a species is present or absent in the region according to the ranges given by Arnold & Burton (1978), is given: + = the species is to be expected; - = the species cannot be expected.

The position of the region within the range of the species is given as follows: c = the region lies (rather) centrally in the range of the species; p = the region is peripheral in the range of the species.

** The Maastricht region (southeastern part of The Netherlands) is inserted in this review because data, which were collected in much the same way as we do, are available. Furthermore the position of the region is interesting in our north-southern transect. These data are derived from Duyghuizen et al., 1976 (unpublished) and from "Lacerta Werkgroep Zuid-Limburg" (Anon., 1977).

TABLE III
Distribution densities in various elements of the landscape at Boulogne-sur-Mer.

	<i>n</i>	<i>Salamandra salamandra</i>	<i>Triturus marmoratus</i>	<i>Triturus cristatus</i>	<i>Triturus alpestris</i>	<i>Triturus vulgaris</i>	<i>Triturus helveticus</i>	<i>Bombina variegata</i>	<i>Alytes obstetricans</i>	<i>Pelobates cultripes</i>	<i>Pelobates fuscus</i>	<i>Pelodytes punctatus</i>	<i>Bufo bufo</i>	<i>Bufo calamita</i>	<i>Hyla arborea</i>	<i>Hyla meridionalis</i>	<i>Rana temporaria</i>	<i>Rana arvalis</i>	<i>Rana dalmatina</i>	<i>Rana esculenta</i> complex
hills	118	11		37	64	39	61		51			2	55	2	8		22			1
swamps	53			1	2	15	35						38	2	7		49	2		1
dunes	42			15	25	17	6		20			6	37	30	15		32	2		
Boulogne-sur-Mer (total)	213	11		53	91	71	102		71			8	120	34	30		103	4		2

n = Number of pools investigated. The other numerals indicate the number of sites. The encountered population densities are given by squares, viz.: open, hatched, blocked and black which means, resp.: the species was observed in 5% of the investigated pools at maximum, in 5 to 15%, in 15 to 40%, over 40%.

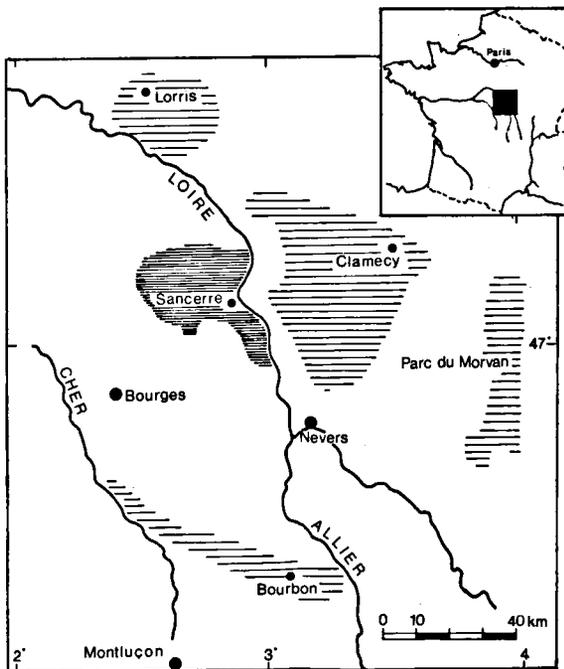


Fig. 2. The Sancerre region and the surrounding regions Lorris, Clamecy, Parc du Morvan and Bourbon. The finely hatched region was elaborately investigated, the widely hatched regions were occasionally inventorized.

the forms within the complex) are very common. These three species occur together in most pools and may be accompanied by other species dependent on the part of the region and the type of pool. *Rana dalmatina* in particular seems to mate here in every pool, no matter how shallow or temporary it may be.

Triturus cristatus is common in the river plain and in the pools in the pastures and fields of the hilly country, but is completely absent on top of and along the slopes of the higher wooded hills of the western fringe of the region.

Bufo bufo is common, in the forests even very common. The shallow embankment of small lakes with less than 0.5 m of water and with *Juncus* sp. or *Scirpus* sp. dominating the vegetation are especially appreciated by this toad for mating. Such a water body in or at the margin of a forest accommodates the highest number of toads.

Hyla arborea is common in the river valley and in the hilly country where we find the species in swamps and in small water reservoirs, often surrounded by a hedge-like vegetation. Like *Triturus*

cristatus, the species is absent in the western fringe of the region.

Rana temporaria is rare here and found to mate exclusively in shallow pools in or along the margin of forests in the western part of the region.

Alytes obstetricans is also rare, probably because of the region's predominantly clayey soil, which is not very suitable for this digging animal. Four populations were found, two housing at castles and the other two at the ruined buildings of abandoned hamlets.

Triturus vulgaris is rare, regarding the number of sites as well as the number of adults these accommodated. The species approaches its southern distribution boundary, and can survive only under optimal conditions which are rarely met here. We

find *T. vulgaris* here only in a special kind of pool, the "newts pool", being an unshaded abundantly overgrown pool (with *Glyceria fluitans*, *Callitriche* sp., *Ranunculus aquaticus*), generally in a meadow.

Bombina variegata has become rare in the region because of the current way of using springs, which has decimated the shallow weedy pools in pastures. The only occurrences found are located along a higher ridge in the western part of the region. The soil is chalky there and water seeps out at various places.

Salamandra salamandra larvae were found commonly in pools of stagnant water in forests and in pools receiving water from a spring, such as the former washing houses found here.

TABLE IV

A: Densities of populations for the various elements of the landscape at Sancerre.
 B: Densities of populations compared to those of the surrounding regions.

	<i>n</i>	<i>Salamandra salamandra</i>	<i>Triturus marmoratus</i>	<i>Triturus cristatus</i>	<i>Triturus alpestris</i>	<i>Triturus vulgaris</i>	<i>Triturus helveticus</i>	<i>Bombina variegata</i>	<i>Alytes obstetricans</i>	<i>Pelobates cultripes</i>	<i>Pelobates fuscus</i>	<i>Pelodytes punctatus</i>	<i>Bufo bufo</i>	<i>Bufo calamita</i>	<i>Hyla arborea</i>	<i>Hyla meridionalis</i>	<i>Rana temporaria</i>	<i>Rana arvalis</i>	<i>Rana dalmatina</i>	<i>Rana esculenta</i> complex
A	river valley	30	1	13	3	10	1					8	5						21	16
	hilly country	77		25		45	3					16	12						58	48
	wooded fringe	20	4			6	2					10					4		11	6
	total region Sancerre	127	5	38	3	61	2	4				34	17				4		90	70
B	Lorris	15	3	2		9		1			1	2	3	5		1		7	12	
	Clamecy	24	1	6	6	1	15	2	5		2	5		5		3		10	16	
	Parc du Morvan	6	1		1	2		3				1		1		3		2	4	
	Bourbon	9	1	1	3		8					1		4		3		3	6	

n = Number of pools investigated. The other numerals indicate the number of sites. The encountered population densities are given by squares, viz.: open, hatched, blocked and black which means, resp.: the species was observed in 5% of the investigated pools at maximum, in 5 to 15%, in 15 to 40%, over 40%.

In addition to the 11 amphibian species we met with in the Sancerre region, also *Pelobates fuscus*, *Pelodytes punctatus*, *Triturus marmoratus* and *Bufo calamita* were expected (see table II). Except for *Pelobates fuscus* all these species, and *Triturus alpestris*, were found in adjacent regions, within 80 km from Sancerre. These regions represent four different types of landscape:

(1) Around Lorris, a narrow river plain immediately along the Loire and beyond which lie higher, sandy terraces which are partly wooded. The wooded stretches are reminiscent of a scenery of old dunes.

(2) Around Clamecy, a gently undulating terrain, underlain by marl, shale and gravel, used mainly for agriculture. Most amphibians occur in the sparse meadows.

(3) Parc du Morvan, a highly dissected massive comparable to the Plateau Central, with altitudes up to 850 m. It is a National Park with picturesque villages, forests, lakes and pastures.

(4) Around Bourbon, the soil is a stony and sandy clay and is calcareous. The scenery shows hills with pastures and many wooded banks, clusters of trees and forest belts. Water seeps out of the hills at a good many places, yielding beautiful pools. It is a charming region.

Table IV part B shows the amphibian distribution within the Sancerre region in comparison to the distributions in adjacent regions. We find: — A group of species that are common to abundant in Sancerre (*Triturus helveticus*, *Rana dalmatina*, *Rana esculenta* complex and *Bufo bufo*) and which are equally present in the adjacent regions. *Triturus cristatus* deserves special attention as it is either common or totally absent, as in Sancerre, displaying a discontinuous distribution. — The rarer species form another group with *Alytes obstetricans*, *Triturus vulgaris*, *Bombina variegata*, *Pelodytes punctatus* and *Bufo calamita*. The striking abundance of *Alytes obstetricans* in Parc du Morvan is explained very well by its preference for a stony bottom. The presence of *Bufo calamita* exclusively in Lorris shows its restraint to sand.

Rana temporaria appears to be abundant in Parc du Morvan, which may be related to the higher altitude of this region.

Triturus marmoratus was found only in the sandy, wooded Lorris region, whereas *T. cristatus* was not found there. The hybrid of these related species, "*T. blasii*", was found in the Bourbon region, pointing to the presence of both parent species there.

Some striking distribution data and biotope preferences in Sancerre and adjacent regions:

— *Triturus vulgaris* is rare and is highly demanding as to its spawning sites. It represents a classic example of a species rarifying towards the margin of its range, finally being replaced by a related species, in this case by *T. helveticus*. Within the large sympatric zone the species apparently replace one another gradually (table II). Going from north to south we find: *Triturus vulgaris* to be abundant and *T. helveticus* to be rare in the south-east of The Netherlands; both species to occur in the Boulogne-sur-Mer region; *T. vulgaris* to be rare and *T. helveticus* to be very common in the Sancerre region.

— The distribution patterns of *Triturus cristatus* and *T. marmoratus* in the Sancerre and adjacent regions form a mosaic. The overlap of the ranges of these species is a zone of some 100 km wide in central France comprising the Sancerre and adjacent regions (except Parc du Morvan). *T. cristatus* is very common in the Sancerre region, whereas *T. marmoratus* is absent there. *T. marmoratus* was found in Lorris, but not so *T. cristatus*. The Bourbon region accommodates both species. Thus, within the zone of overlap the distributions of the species prove to be discontinuous.

— *Rana temporaria* is rare in Sancerre and occurs exclusively in or at the margin of forests, a habitat which is different from that in more northern regions. This restriction to rather cool forests may be explained as an ecological adaptation to the — generally — warmer circumstances in the southern part of its range. Only under such favourable circumstances *R. temporaria* is not replaced by its southern substitute, *R. dalmatina*, which is common already in Sancerre.

2.3. The Monluçon region. — Because of the great variety in landscape we divide the region into seven subregions (fig. 3), based upon differences in altitude and relief, as follows:

— Vichy is a strongly undulating area with clayey soil. Springs occur along the slopes. The pools occur between 450 and 500 m.

— Gannat is a flat region west of the river Allier. It is used mainly for agriculture. The country furnishes only a few suitable spawning sites. There are many reservoirs stocked with fish. The pools all lie at altitudes about 300 m.

— Montluçon-South has hills which may be high and steep, especially along the right bank of the river Cher. The pools lie mostly in pastures. The range in altitudes of the pools is great (360 to 630 m).

— Boussac-East is a rather undisturbed hilly area. The amphibian sites were found at altitudes from 340 to 480 m.

— Boussac-West is a north-south running chain of hills with occasional steep slopes. The soil is stony. Most amphibians are encountered in springs at farms, in hamlets or in forests, and between altitudes of 340 and 590 m.

— Nassigny, immediately west of the river Cher is an only slightly undulating area. The amphibian sites were found between 220 and 270 m.

— Bourbon. This subregion was mentioned before, as it is adjacent to the region of Sancerre

and visited in 1977. In the present inventories of 1978, data of a good many sites are added to those previously known.

It must be noted that most pools were visited only once during June and July and therefore some species may have been missed. *Bufo calamita*, *Pelodytes punctatus* and *Pelobates fuscus* are species expected to occur in the region (table II) but which have not been found.

The actually observed distributions, divided with regard to the subregions, are given in table V.

We find a striking distinction between Vichy and the western subregions across the river Allier. East of the Allier *Triturus cristatus* and *Bombina variegata* are common and *Triturus alpestris* is abundant, but west of the Allier these species are absent. Further westward *B. variegata* reappears but *T. cristatus* and *T. alpestris* do not. The distribution pattern of *B. variegata* here may be explained by the character of the landscape and the type of pools. *B. variegata* can be found in the pools at springs in hilly country which are frequent in Vichy, lack in Gannat and can be found again along the steep slopes of Boussac.

The present data of *T. alpestris* confirm the known distribution boundary running along the Loire and Allier (after Thorn, 1968). The abundance of this species in Vichy, immediately at the border of its range may be explained by the suitability of this strongly undulating terrain with the spring-fed pools lying rather high.

Triturus cristatus and *T. marmoratus* are replacing each other. Only in Bourbon both species co-exist and hybridize. *T. cristatus* appears to be common in Vichy, Bourbon and Nassigny and is lacking in the rest of the region. *T. marmoratus* increases in number from Gannat to the west. It is absent in Vichy and Gannat, rare in Montluçon-South, common in Boussac-East and very common in Boussac-West.

Triturus vulgaris: Having found the species only twice, just at its southern distribution boundary, it appears to be even rarer than in the Sancerre region.

Hyla meridionalis has been found in one pool (larvae). From this observation it appears that the species is occurring more northward than previously known. The related species, *H. arborea*,

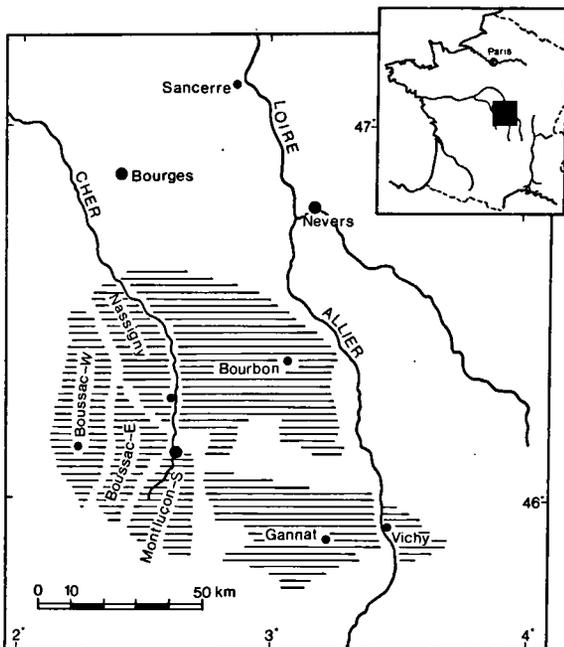


Fig. 3. The Montluçon region, divided into: Vichy, Gannat, Montluçon-South, Boussac-East, Boussac-West, Nassigny and Bourbon. All regions were occasionally inventorized.

TABLE V
Densities of populations of the subregions of the Montluçon region.

	<i>n</i>	<i>Salamandra salamandra</i>	<i>Triturus marmoratus</i>	<i>Triturus cristatus</i>	<i>Triturus alpestris</i>	<i>Triturus vulgaris</i>	<i>Triturus helveticus</i>	<i>Bombina variegata</i>	<i>Alytes obstetricans</i>	<i>Pelobates cultripes</i>	<i>Pelobates fuscus</i>	<i>Pelodytes punctatus</i>	<i>Bufo bufo</i>	<i>Bufo calamita</i>	<i>Hyla arborea</i>	<i>Hyla meridionalis</i>	<i>Rana temporaria</i>	<i>Rana arvalis</i>	<i>Rana dalmatina</i>	<i>Rana esculenta</i> complex
Vichy	9			4	8		8	3	2								1		4	6
Gannat	10						6						2				3		3	5
Montluçon-S.	15		2				11		5						1		4		9	2
Boussac-E.	10		2				10									1			6	6
Boussac-W.	12		7				11	2	2				1		1				10	8
Nassigny	7			2			6	1	1										4	3
Bourbon	77	4	5	22		2	34	4	3				4		12		9		32	44
total region Montluçon	140	4	16	28	8	2	91	10	13				7		14	1	17		68	74

n = Number of pools investigated. The other numerals indicate the number of sites. The encountered population densities are given by squares, viz.: open, hatched, blocked and black which means, resp.: the species was observed in 5% of the investigated pools at maximum, in 5 to 15%, in 15 to 40%, over 40%.

appears to be common in the neighbourhood. Whether or not these species influence each others distribution, and if so, in what manner, cannot be ascertained from the present data.

2.4. Vienne and adjacent regions. — With respect to elements of the Vienne landscape, difference is made between:

- occurrences on plateaus (poor soils, pH of surface water about 5, poor soil permeability, oak and birch dominant in the forests), in water reservoirs and cart tracks;
- occurrences on slopes in ponds at springs in general, small swamps along brooks and cattle watering places;
- occurrences on terraces in small water reservoirs and springs;
- occurrences in the valley plain, a broad even plain with ditches, used for agriculture.

The degree in which amphibians occur in the various elements of the landscape is given in table VI part A, showing slopes, with their great variety of spawning sites, to have the largest variety of species.

Rana dalmatina appears to be the commonest species at Vienne with 91 observed occurrences. Like in the Sancerre region, the species mates in all kinds of pools. Just as in the other regions a preference was apparent concerning the deposition of the eggs, which are preferably attached to dead branches immediately below the water surface. Perennial plants, such as *Carex*, *Juncus*, *Scirpus* or *Rumex* are second choice.

Rana temporaria appears to be rare in Vienne. Eggs and larvae are found only in pools along the slopes and on the plateaus, in general in the highest parts of the region. All spawning sites were located in or near forests.

TABLE VI

A: Densities of populations for the various elements of the landscape of the Vienne region.
 B: Densities of populations compared to those of the adjacent regions.

	<i>n</i>	<i>Salamandra salamandra</i>	<i>Triturus marmoratus</i>	<i>Triturus cristatus</i>	<i>Triturus alpestris</i>	<i>Triturus vulgaris</i>	<i>Triturus helveticus</i>	<i>Bombina variegata</i>	<i>Alytes obstetricans</i>	<i>Pelobates cultripes</i>	<i>Pelobates fuscus</i>	<i>Pelodytes punctatus</i>	<i>Bufo bufo</i>	<i>Bufo calamita</i>	<i>Hyla arborea</i>	<i>Hyla meridionalis</i>	<i>Rana temporaria</i>	<i>Rana arvalis</i>	<i>Rana dalmatina</i>	<i>Rana esculenta</i> complex
A	plateau	81	8	2	29		43	2					6				3		45	25
	slope	75	11		3	15	23	13	14				9				5		26	31
	terrace	14	3		2	4	6	1	4				1						6	6
	valley plain	28	1				6		1				1						14	12
	total Vienne region	198	23	7	48		78	16	19				16				8		91	74
B	Montélimar	40	3				13		13	2		5	10	4	7	1				4
	Privas	39	8		5	1	20	4	21				8	1			4			11

n = Number of pools investigated. The other numerals indicate the number of sites. The encountered population densities are given by squares, viz.: open, hatched, blocked and black which means, resp.: the species was observed in 5% of the investigated pools at maximum, in 5 to 15%, in 15 to 40%, over 40%.

Bufo bufo is found in all four elements of the landscape, be it mainly along the slopes. Compared to Sancerre, preferential biotopes exist evidently, attracting thousands of males and females for mating. It is remarkable that here like elsewhere *B. bufo* is absent in newly made pools where *Rana dalmatina*, members of the *Rana esculenta* complex and *Triturus helveticus* do mate already. From these observations it appears that an essential requisite of *B. bufo* as to its spawning site is a mature, permanent pool. Possibly these demands are the origin of the frequently mentioned (amongst others by Heusser & Ott, 1968) "loyalty" of *B. bufo* to the spawning site.

Three *Triturus* species occur, of which *T. cristatus* appears to be rare. This species shows a clear

biotope preference in this region: unshaded pools of at least 12 m², and sufficiently deep to guarantee permanence. All *T. cristatus* sites are marked by a well-developed aquatic vegetation, consisting of *Glyceria fluitans*, *Callitriche* sp., *Mentha aquatica* and *Potamogeton* sp. Only few *cristatus* specimens were found at each site, whereas both other *Triturus* species appeared to be abundant. In this manner *T. cristatus* always occurred together with large *T. alpestris* and *T. helveticus* populations in the typical "newts pool".

Bombina variegata is notably a species of the hills and appears to have a specific choice of biotope here, viz.: shallow pools in pastures which are fed by a spring. The shallow water of unshaded pools is quickly warmed up in sunny weather and

their location near a spring prevents them from drying up. Frequently *B. variegata* specimens are the only amphibians in such a biotope, occasionally together with *Alytes obstetricans*.

Members of the *Rana esculenta* complex (see fig. 5 for the forms within the complex) can be seen and heard in all parts of the landscape and in all types of pools, even in the temporary pools and along brooks. According to local people the species was even more common in the past (up to ten years ago), especially in running waters. Likewise, people told about the former presence of *Hyla* species. Both species, *arborea* and *meridionalis*, could be expected (table II), but were not found.

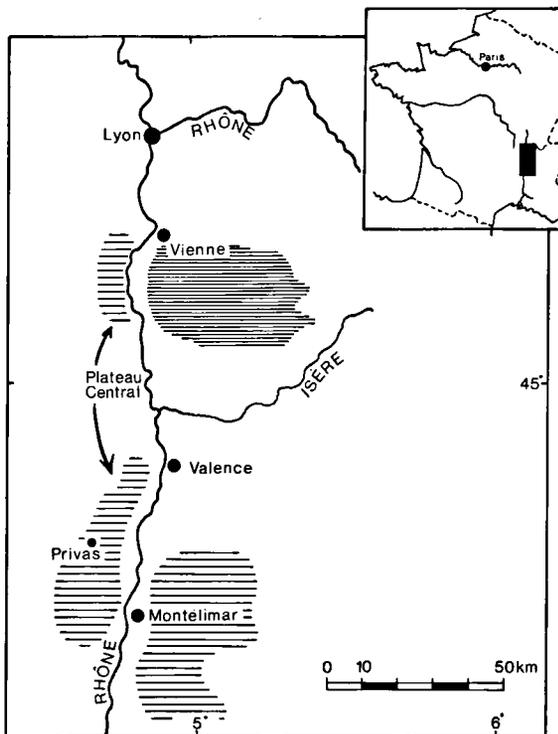


Fig. 4. The Vienne region and adjacent regions, Montélimar and Privas (Plateau Central). Finely hatched: elaborately investigated; widely hatched: only occasionally inventoried.

Montélimar region. — Going southwards from the Vienne region (fig. 4), the scenery changes rapidly. Whereas in the surroundings of Vienne the climate is still strongly influenced by the Alps, 100 km to the south, in the Montélimar region, Mediterranean influences in the climate are dominant already, making it dryer and warmer. More-

over, there are differences in topography and petrography. Whereas pools and other surface waters are still abundant in the surroundings of Vienne, hardly any stagnant surface water can be found in the sandy region of Montélimar, only an occasional brook or spring. It is not surprising therefore that there are many distribution boundaries of amphibian species between Vienne and Montélimar (fig. 1). This causes a striking difference in the composition of the amphibian populations of the Vienne area and Montélimar, as can be seen in table VI, part B.

Two *Triturus* species, *T. cristatus* and *T. alpestris*, are lacking in Montélimar, a third, *T. helveticus*, is less common. Swampdwellers like *Rana temporaria* have disappeared. *Bombina variegata*, the species of the pools on slopes with clayey soil, does not occur here. Those species that appeared to prefer the dunes in the Boulogne-sur-Mer region, viz.: *Hyla arborea*, *Bufo calamita* and *Pelodytes punctatus*, do occur however, as does *Pelobates cultripes* and *Hyla meridionalis*. In the Rhône valley this represents a more northern occurrence of *P. cultripes* than previously known. The presence of *Hyla meridionalis* and *Hyla arborea* in the same area shows coexistence of both species, like in Montluçon.

Privas region. — The Rhône separates the Plateau Central and the foothills of the Alps geologically and climatologically. The Plateau Central is higher and cooler. This massive consists mainly of igneous and metamorphic rocks. Surface waters in the Plateau Central comprise water reservoirs, springs and brooks. The population of amphibians of the Plateau Central reflects again the climatological or geological differences, or both, when compared to those of Vienne or Montélimar (table VI, part B). Newts are numerous, *Rana temporaria* is back again and, notably, also *Alytes obstetricans*, preferring stony ground so much, is more abundant than ever here.

Some important distribution data in these regions: Actually observed southern distribution boundaries of *Triturus cristatus*, *Triturus alpestris* and *Rana temporaria* run through the investigated area. Concerning *T. cristatus*, the species occurs rarely at

the south of its range, and in Vienne the species only survives in very suitable sites. On the Plateau Central at about the same latitude as Vienne, but at a higher altitude, *T. cristatus* is more common, in number of individuals per pool as well as in number of localities. Thus the suitability of the Vienne region is probably less for *T. cristatus* because of the warmer climate. *Rana temporaria* is sparsely present and was found only at higher altitudes. According to information from local people a decline of amphibians is apparent.

IV. DISCUSSION

1. Population densities

The phenomenon that a species is common in the centre of its range could not be confirmed for all species, as is shown in table II. *Pelodytes punctatus* and *Bufo calamita* for instance are lacking in Sancerre, Montluçon and Vienne. Their absence there is the more striking as the regions lie rather centrally in their ranges. The species may be absent in regions with mainly clayey or peaty soil around Sancerre and Vienne. However, in the sandy terrains as the dunes of Boulogne-sur-Mer and in the Montélimar region these species are present. The distribution of *Bombina variegata* in France appears to be controlled by the nature of the landscape as well. Its spawning sites are notably unshaded pools at springs along slopes. These specific *B. variegata* biotopes occur in all regions except Montélimar. In this way we find a more patchy distribution pattern for those species which are restricted to a certain kind of soil, or other features of the landscape. Another group of species does not show this specific preference for a certain terrain, viz.: *Bufo bufo*, *Rana* species and *Triturus* species.

A decline can be observed of the members of the *Rana esculenta* complex, of the *Hyla* species and of amphibians in general. Alarming news came from people of Sancerre and Vienne and from the dép. Mayenne (Vallée, pers. comm.). France seems to lag behind the Netherlands in this respect, where a decline starting in the sixties was followed by a recovery in the seventies.

Two current explanations of this impoverishment and the subsequent recovery are:

— The impoverishment was caused by destruction of the environment, notably water pollution by agricultural poisons. The recovery followed upon the amelioration of the water quality after the prohibition of the most heavy poisons (D.D.T. and others) and the introduction, on a large scale, of water purification (Hillenius, pers. comm.).

— Many amphibians died in a severe and prolonged frost period early 1963. As amphibians reach sexual maturity only after a rather long time (at least two years), restoration is a long-term process.

As in France the attack on the environment started out later than in The Netherlands, and as the decline of the amphibian populations also lags behind, the pollution hypothesis gains ground. Moreover, the long and severe frost period in the beginning of 1979 did not destroy amphibian populations to any extent, as we could observe from several well-known areas in France and in The Netherlands.

The *Rana esculenta* complex

Fig. 5 shows both species, *R. ridibunda* and *R. lessonae*, and the hybrid "*R. esculenta*" to exist in central and southeastern France. "*R. esculenta*" appears to be more common than *R. ridibunda*, even much more common than *R. lessonae*. The *ridibunda* specimens from Sancerre are less typical than the measured specimens from Portugal. The measured *lessonae* specimens from both regions in France are less typical than the *R. lessonae* measured from Poland.

Arnold & Burton (1978) give a zone in central and northwestern France where *R. ridibunda* does not exist. From our inventories it may be clear that such a zone is not likely, although a zone exists where the *ridibunda* characteristics are less clear.

2. Various kinds of sympatry

The population densities in the regions where two related species coexist will be discussed for the following pairs of species: *Triturus vulgaris* — *T. helveticus*, *Rana temporaria* — *R. dalmatina* and *Triturus cristatus* — *T. marmoratus*.

The following regions are considered in particular: Boulogne-sur-Mer, Sancerre, Bourbon, Mont-

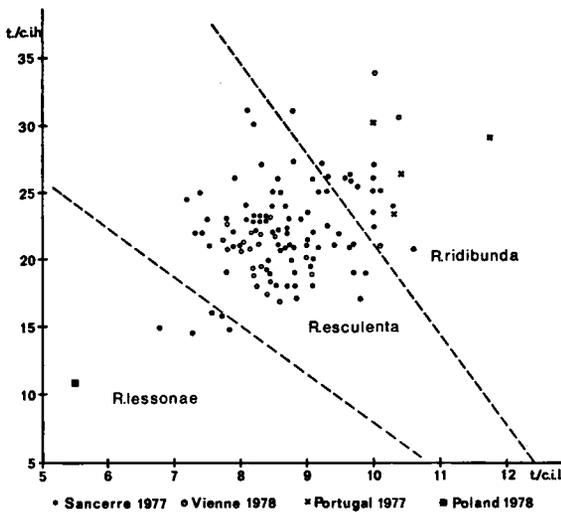


Fig. 5. Scores of morphometric observations of individuals of the *Rana resculenta* complex in Sancerre, caught in June 1977 and in Vienne, caught in May and June 1978. Also included, for comparison, are individuals of *Rana ridibunda* from Portugal (1977) and a *Rana lessonae* from Poland (1978).
 t/c.i.h. = tibia length/callus internus height.
 t/c.i.l. = tibia length/callus internus length.
 - - - - = boundary line between two forms of the *Rana resculenta* complex after Wijnands & Van Gelder (1976). They found these morphometric boundary lines for edible frogs from the Netherlands in combination with differences in protein composition.

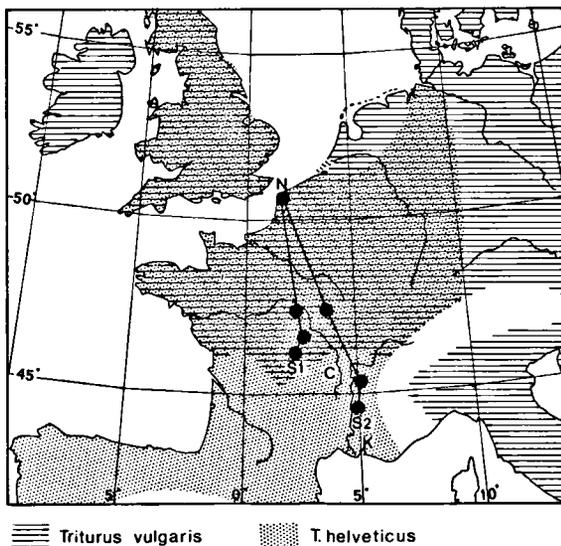


Fig. 6. Distribution of *Triturus vulgaris* and *T. helveticus* after Thorn (1968). C concerns observations by Cantuel (1949), K concerns an observation by Knoepffler (in Anon., 1978). The presently investigated regions, along two north-south running transects, are indicated.

luçon, Parc du Morvan, Vienne and Montélimar. These regions may be placed along two slightly diverging lines, N-S₁ and N-S₂, running southward from Boulogne-sur-Mer; the sequence of N-S₁ being: Boulogne-sur-Mer, Sancerre, Bourbon, Montluçon. For N-S₂ the sequence is: Boulogne-sur-Mer, Parc du Morvan, Vienne and Montélimar. These lines partly run through sympatric areas of species pairs mentioned above (see figs. 6, 8 and 9).

Triturus vulgaris — *T. helveticus*

T. vulgaris expanded from a Würmian centre of distribution, probably somewhere in eastern Europe, over part of Scandinavia, reaching Great Britain, Ireland and, going southward in western Europe, central France. Observations on the Plateau Central (Cantuel, 1949) and in southeastern France (data from Becker & Knoepffler in Anon., 1978) point to a more southern distribution in the past (fig. 6). *T. vulgaris* is very common in the centre of its range, for example in southern Scandinavia (Gislén & Kauri, 1959), in the southwestern part of the G.F.R. (Feldmann, 1975; Glandt, 1978) and in The Netherlands (Van de Bund, 1964). The species is also common in the Boulogne-sur-Mer area. Going southward, the species becomes rare in Sancerre and the Parc du Morvan and very rare in Bourbon (see fig. 7, which shows the encountered population densities along two north-south running transects). *T. vulgaris* was not encountered in Vienne and Montluçon.

T. helveticus is the closest relative of *T. vulgaris*. *T. helveticus* expanded probably from the Iberian peninsula after the cold of the Würm. *T. helveticus* and *T. vulgaris* have a large sympatric area. Within this area the species replace one another gradually (table II) but they do mate in the same pools. Under natural circumstances hybridization does not occur, due to an ethological barrier (Halliday, 1975). The biotope preferences in the area of sympatry appear to be similar to those in the allopatric areas, only the species are more fastidious when they become scarce. In this manner *T. vulgaris* occurs only in the very suitable "newts pools" at the southern fringe of its range. The lack of notable indications of competition

between *T. helveticus* and *T. vulgaris* and the absence of pronounced geological or topographical obstacles at the distribution boundaries, together with the decline of the species along with a gradual rising of the average temperature, suggest a further southward expansion of *T. vulgaris* from central France to be limited by climatological circumstances.

A gradual decline towards the distribution boundary may be a climatologically determined characteristic, resulting in a diffuse boundary.

Rana temporaria — *R. dalmatina*

The range of *R. temporaria* fails to reveal a clear centre of distribution. The species is widespread and can maintain itself very well under northern climatic circumstances. During the glacial

ages *R. temporaria* will have occurred further northward than most other species and the populations in the various refuges were therefore probably poorly isolated. This is also suggested by the great morphological variability, not markedly discontinuous, within the species. After the Würm the expanding populations reached northern Scandinavia and Ireland. The southern fringe of the range receded to the north, and only relict populations in the higher, cooler, regions survived in the south. The continuous range of *R. temporaria* has its southern border in central France now. Farther away from the distribution boundary, *R. temporaria* is a very common species, for example in the southern part of the G.F.R. (Zuiderwijk, 1979), in southern Scandinavia (Gislén & Kauri, 1959) and in The Netherlands (Van de Bund, 1964). In the northernmost region in fig. 7, Boulogne-sur-Mer, *R. temporaria* is still as common as in the rest of the central part of its range. The species is rare in Sancerre, whereas in the Parc du Morvan, at the same latitude but at a higher altitude, the species is more common. In areas south of Sancerre, e.g. Bourbon and Montluçon, *R. temporaria* is not common, but not as rare as in Sancerre. This may be accounted for by their altitude and the influence of the Plateau Central where the species is common. *R. temporaria* does not occur in Montélimar, where southerly circumstances prevail more than in any of the other regions.

Of the species related to *R. temporaria*, *R. arvalis* and *R. dalmatina* occur in the investigated regions. *R. arvalis* and *R. dalmatina* are vicarious species. *R. dalmatina* expanded from the Balkans (perhaps also from Italy). *R. dalmatina* and *R. temporaria* have an extensive area of sympatry. The breeding season and biotope preferences appear to overlap. Couples of *R. dalmatina* were found side by side with croaking *R. temporaria* males (at Vienne on March 14, 1978). Geisselmann et al. (1971) do not consider hybridization probable under natural circumstances. The degree of occurrence and the biotope preferences are not suggestive of important competition between the species. The degree in which *R. temporaria* is present in any of the investigated regions in France is determined by present-day climatological and

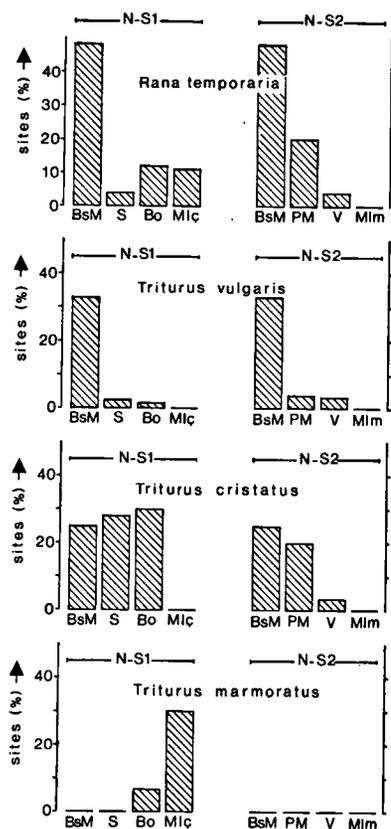


Fig. 7. Population densities of *Rana temporaria*, *Triturus vulgaris*, *T. cristatus* and *T. marmoratus* from north to south. The height of a column gives the occurrence of the species as percentage of the total of investigated pools in a region. The regions are, from left to right: N-S1: Boulogne-sur-Mer (BsM), Sancerre (S), Bourbon (Bo), Montluçon (Mlç); N-S2: Boulogne-sur-Mer (BsM), Parc du Morvan (PM), Vienne (V), Montélimar (Mlm).

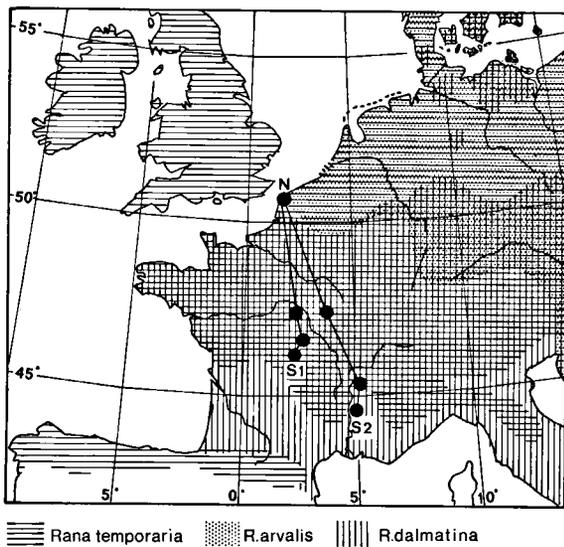


Fig. 8. Distribution of *Rana temporaria*, *R. dalmatina* and *R. arvalis* after Arnold & Burton (1978). The presently investigated regions, along two north-south running transects, are indicated.

topographical circumstances. Having had a more southern extension in former days, the species may maintain itself in the boundary zone by the choice for forests at the southern fringe of its range.

As the observations of *R. arvalis* were too few, the pairs *R. arvalis* — *R. temporaria* and *R. arvalis* — *R. dalmatina* cannot be discussed. The latter pair used to have a larger sympatric area: relict populations of *R. dalmatina* are found in northern Germany and southern Scandinavia, situated north of its continuous range and within the range of *R. arvalis* (fig. 8). An investigation of their mutual influences might be interesting.

Triturus cristatus — *T. marmoratus*

T. cristatus expanded from the Balkan refuges after the Würm. The species reached northern Scandinavia and England but did not reach Ireland. In western Europe *T. cristatus* expanded southward to the line Arles—Geneva, with an offshoot to the south covering the Plateau Central (Arnold & Burton, 1978), or, according to Thorn (1968), with an isolated relict population on the Plateau Central suggestive of an earlier, more southward, expansion. The distribution given by Thorn is based, amongst others, on observations by

Cantuel (1949). Care must be taken, however, since the previous investigations carried out on the Plateau Central were rather incomplete. My own occasional observations on the Plateau Central together with systematic investigations north of it, and east of the Rhône (fig. 9), allow local precisions of the distribution boundary given by Thorn and seem to point to a continuous range.

T. cristatus is less common within its range than, for example, *Triturus vulgaris* and *Rana temporaria*. In southern Scandinavia (Gislén & Kauri, 1959), in the south of the G.F.R. (Feldmann, 1975) and also in the southeastern part of The Netherlands (Maastricht region, table II) the species is not common and occasionally even rare, which is attributed to loss of biotopes through pollution, re-allotment and urbanization (Honegger, 1978). Unlike *T. vulgaris*, *T. cristatus*, being a large newt, makes special demands upon the size of its spawning site and the water depth. As shown in fig. 7, along the N-S₂ transect, *T. cristatus* appears to be common in the more or less centrally located Boulogne-sur-Mer region, and common in the relatively high Parc du Morvan region, but rare in Vienne and absent in Montélimar. This distribution pattern along the N-S₂ transect appears

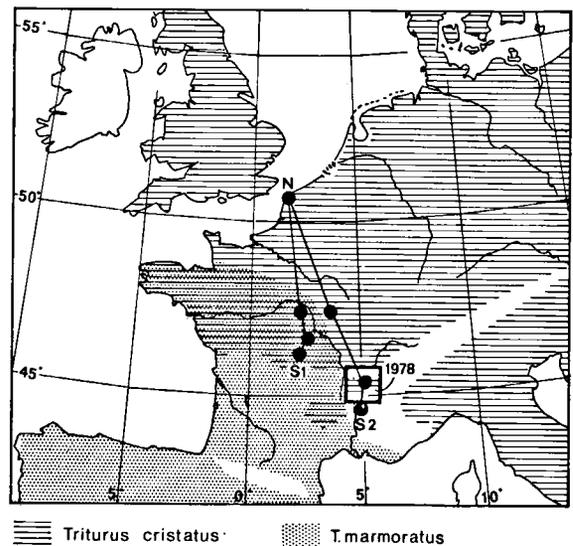


Fig. 9. Distribution of *Triturus marmoratus* and *T. cristatus* after Thorn (1968), completed with personal observations (1978) for *T. cristatus* at Vienne and the Plateau Central. The presently investigated regions, along two north-south running transects, are indicated.

to be similar to the gradual decrease of other species reacting upon climatological circumstances. Along the N-S₁ transect however, *T. cristatus* increases in number in Sancerre and, even more, in Bourbon, but is lacking suddenly in Montluçon. This distribution is quite contrary to the north-south transects discussed so far. The N-S₁ transect crosses the distribution boundary of *T. marmoratus*, the nearest related species of *T. cristatus*, just north of the Loire (fig. 9). Sancerre, Bourbon and Montluçon all lie within the zone of overlap of the ranges of these related species.

T. marmoratus expanded northwards from the Iberian peninsula after the Würm, reaching Normandy and part of the Paris basin, and stayed west of the Rhône, except for the southernmost part where it did cross the river (Anon., 1978). Cantuel (1949) reported *T. marmoratus* from the Plateau Central except in the highest parts.

Spawning sites of *T. marmoratus* and *T. cristatus* are similar. Both are called species of plains and hilly country by Ricqlès (in Anon., 1978). Thorn (1968) mentions stagnant surface water and sufficiently deep ponds for both species; in addition he mentions pools in swamps and moorland and even watering pools for *T. marmoratus*. Vallée (1959) found no differences in spawning sites. An important difference, however, is presented by the more aquatic way of life of *T. cristatus* (Thorn, 1968). Hybrids occur in pools where both species reproduce. Hybrids are always scanty, because of the low fertility in the initial stages of development; moreover, male hybrids are sterile (Lantz, 1947). Hybridization is not hampered by ethological barriers (Vallée, pers. comm.).

The above-mentioned similarities in ethology and ecology suggest strong competition.

In fig. 7 a general survey of the abundance of both species is given. Fig. 10 shows the data from their sympatric area more precisely (data from the Salbris area, 1978, according to J. Schoorl, unpublished, are added). It is clear from the figure that *cristatus* and *marmoratus* occur mostly at separate localities. In the Lorris and Salbris regions, accommodating only *T. marmoratus* (fig. 10), this species occurs in pools in forests. At one locality between both regions *T. cristatus* occurs in open country. In the Sancerre region *T. cristatus* is com-

mon in the river plain and the open hilly pasture lands, but it is lacking in the wooded western fringe. In Boussac-West, Boussac-East, and in Montluçon-South, where *cristatus* is absent and *marmoratus* is common, the abundance in pools at springs along slopes is striking. In the Bourbon subregion, accommodating both species, we recognize again the preference of *marmoratus* for shade and springs and of *cristatus* for open country: 21 out of 26 *cristatus* sites were unshaded and 7 were fed by a spring, whereas 3 out of 5 *marmoratus* sites were shaded and 4 were fed by a spring.

In conclusion: since hybrids of *T. cristatus* and *T. marmoratus* are unsuccessful and since an

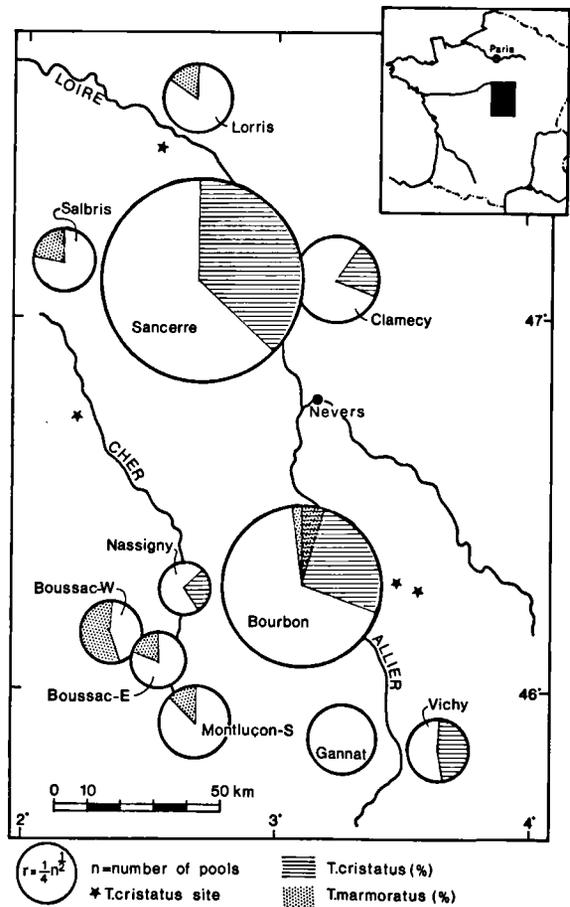


Fig. 10. Densities of populations of *Triturus cristatus* and *T. marmoratus* in the Sancerre region and surrounding regions, and in the Montluçon subregions. Note: the radius of each circle is related to the number of pools investigated. The size of the segments is proportional to the percentages of occurrences of *T. cristatus* and *T. marmoratus*, respectively.

ethological barrier preventing hybridization does not exist, it is advantageous for the species to occupy separated spawning sites. The evident restriction of *marmoratus* to forests on the one hand and the notable preference of *cristatus* to open pools on the other is to be found only within the area of sympatry and not in allopatric areas. In view of the above-mentioned arguments we explain their restriction to certain, separated, biotopes as ecological displacement, caused by severe competition and enhanced by the reduced fitness of the hybrids. The preference to forests of *T. marmoratus* appears to be plausible: *T. marmoratus* adults never stay in the pools during winter, whereas *T. cristatus* adults may do so; *marmoratus* juveniles live on land, but *cristatus* juveniles frequently live in water; after the breeding season *marmoratus* leaves the pool sooner than *cristatus*. Therefore forests are more suitable to *T. marmoratus* as they offer more hiding places and greater humidity to animals living on land.

Assuming ecological displacement caused by competition as discussed in the foregoing, the distribution within the Bourbon subregion can be explained. The area has changed much over the last 80 years due to the construction of watering places for cattle and by transforming springs into drinking ponds (Vallée, 1959). Increase of agriculture was reached by felling of forest, even enhanced later by re-allotment (pers. comm. of inhabitants). These measures favoured the number of spawning sites for *T. cristatus*. This is reflected in the current distribution pattern, showing an expansion of *cristatus* at the expense of *marmoratus*. In 5 pools out of 70 we found a few specimens of *marmoratus*. In these *marmoratus* sites many *cristatus* specimens were present. Moreover, these pools are surrounded by *cristatus* sites. For example: in a pool in pasture land, 12 × 6 m² and with an average depth of 0.6 m, we calculated the *cristatus* adult population to be 482 ± 78 (June 3rd, 1978, by means of capture and recapture according to Bailey, 1952). During capture and recapture only one *marmoratus* adult (and two hybrids) were found.

Within their area of sympatry the distribution boundaries of *T. cristatus* and *T. marmoratus* are sharp, and appear to be determined by competition

3. Relationship phenomena

Several variables allow investigation into the relationship of species in sympatric areas, viz.: success of hybridization, degree of isolation, size of the sympatric area and distribution densities within it.

We found the most closely related species to be abundant within a small sympatric area resulting in sharp distribution boundaries, whereas the less closely related species gradually replace each other within a large sympatric area, resulting in diffuse distribution boundaries.

These connections between degree of relationship, size of the sympatric area, and population densities within the sympatric area, possibly form a certain pattern. Considering these phenomena for some other pairs of species, we can see how regular the pattern, found for the species under study here, generally is. Taking successful hybridization as a measure of relationship, we have listed the species pairs which are discussed in the foregoing and some other pairs of species which are sympatric in Europe in table VII.

Leaving the problematical *Rana esculenta* complex out of consideration, it is clear from the table that: (1) the size of the sympatric area is related to the character of the distribution boundary; (2) the success of hybridization decreases when the size of the sympatric area increases. Especially the distribution pattern of the *Bombina* species, in and near the zone where they contact, is convincing in this respect. Where *B. bombina* and *B. variegata* meet, a narrow hybrid zone exists between the two parent populations. Like *Triturus cristatus* and *T. marmoratus*, the species are abundant up to the border and then come to a sudden stop.

Less related species, viz. *Bufo viridis* — *B. calamita* and *Hyla arborea* — *H. meridionalis* are partly overlapping, not very abundant in the sympatric area, and show a diffuse distribution boundary. Widely overlapping species show very diffuse boundaries: *Triturus vulgaris* and *T. helveticus* replace one another very gradually; *Rana temporaria* diminishes gradually and of *R. dalmatina* only few populations are reported in boundary regions.

TABLE VII

Phenomena connected with relationship listed for some related pairs of species of Europe.

Pairs of species	Relationship			Distribution	
	natural hybrids	experimental hybrids	fertility hybrids	size of sympatric area	character of the boundary
<i>Rana lessonae</i> <i>R. ridibunda</i>	+++	yes ¹⁾	+	++++	? (not clear)
<i>Bombina bombina</i> <i>B. variegata</i>	++ ²⁾	yes ²⁾	+ ²⁾	— ²⁾	very sharp
<i>Triturus cristatus</i> <i>T. marmoratus</i>	+	yes ³⁾	only ♀♀ ³⁾	+	sharp
<i>Bufo viridis</i> <i>B. calamita</i>	? ⁴⁾	larvae ⁴⁾	—	++ ⁵⁾	gradual ⁴⁾
<i>Hyla arborea</i> <i>H. meridionalis</i>	—	— ⁶⁾	—	++	gradual
<i>Triturus vulgaris</i> <i>T. helveticus</i>	—	+ ⁷⁾	—	+++	very gradual
<i>Rana dalmatina</i> <i>R. temporaria</i>	—	— ⁸⁾	—	++	very gradual ⁹⁾

The table is made from data out of our own investigations and from literature data, as follows:

¹⁾ Wijnands (1979), Hotz (1974); ²⁾ Arntzen (1978); ³⁾ Lantz (1947); ⁴⁾ Flindt & Hemmer (1967a & b); ⁵⁾ Arnold & Burton (1978); ⁶⁾ Knoepffler (pers. comm); ⁷⁾ Spurway & Callan (1960); ⁸⁾ Geisselmann et al. (1971); ⁹⁾ Gislén & Kauri (1959).

ACKNOWLEDGEMENTS

I would like to thank everyone who rendered me assistance in my work. Firstly Dr. D. Hillenius and Prof. Dr. J. H. Stock of the Institute of Taxonomic Zoology of the University of Amsterdam, for enabling the investigation. Dr. S. Pinkster assisted greatly in supplying measuring devices; Mr. H. Mittelberg made perfect fishing nets. Fertile discussions with D. Hillenius, Pim Arntzen and Gerard Kruse are gratefully mentioned. Thanks are also due to Tom Gerats, Jaap Schoorl, Wim Bergmans and to all workers at the Ambletuse field station for their pleasant co-operation. I thank Prof. Dr. J. H. Stock for his critical review of the manuscript.

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Received: 31 January 1980