THE DISTRIBUTION OF TRITURUS ALPESTRIS (AMPHIBIA, CAUDATA) AT ITS NORTHERN LIMIT, IN SOUTH DENMARK

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ABSTRACT

The northernmost populations of *Triturus alpestris* live in South Denmark (Southeast Jutland) where it has been recorded west, southwest and south of the town of Åbenrå and in five forest areas in the southeasternmost part of Jutland. Its occurrence in Denmark is most probably natural and not due to an introduction. The northern limit of the range of *T. alpestris* is not a climatic limit. Open farmland made during the last two to four centuries seems to form a barrier preventing *T. alpestris* from dispersing further north. It has been registered in 120 ponds, however, it has disappeared from at least 10 of these which have been filled in or have dried up. Of the 110 existing ponds 87 are in the main region near Åbenrå, 23 are in the smaller southeastern region. In Denmark the species has only been found in ponds in association with deciduous forests and in pastures or uncultivated fields within distances of 80 m from deciduous forests. The breeding ponds are usually small with a surface smaller than 200 m². In Denmark (altitude 66m) the migration to the breeding pond takes place some 1-2 weeks later than in Central Germany (altitude 70m), roughly at the end of March.

INTRODUCTION

The Alpine newt, Triturus alpestris (Laurenti 1768) has its main distribution in Central and East Europe, with a more scattered range in South Europe. Its northernmost natural occurrence is in South Denmark. In England a number of introductions have been made, the northernmost which has been published is from Sunderland, Northeast England (Banks, 1989) which is ca. 15km south of Åbenrå (Aabenraa), southeastern Jutland (Jylland). It was verified and reported by Bisgaard (1949a, b). Shortly after, it was found at three other localities in the area of Åbenrå. Consequently, in 1951 it became totally protected by law in Denmark. From 1951 to 1974 it was not being paid much attention and the question was whether it still lived in Denmark and to what extent.

In that connection a working group named Bjergsalamandergruppen ("The Alpine Newt Group") was formed. Thus, since 1975 the group has performed extensive investigations throughout southeastern Jutland in order to establish the Danish distribution of *T. alpestris* and to protect the species and its habitats (Bisgaard, 1982, 1984; Bisgaard et al., 1979a, b, 1980). The following results are presented on behalf of the working group.

In this paper emphasis will be put on the Danish distribution of *T. alpestris*. It is compared with that of North Germany. Some other characteristics of its habitat selection are provided. On the basis of its current distribution and the historical

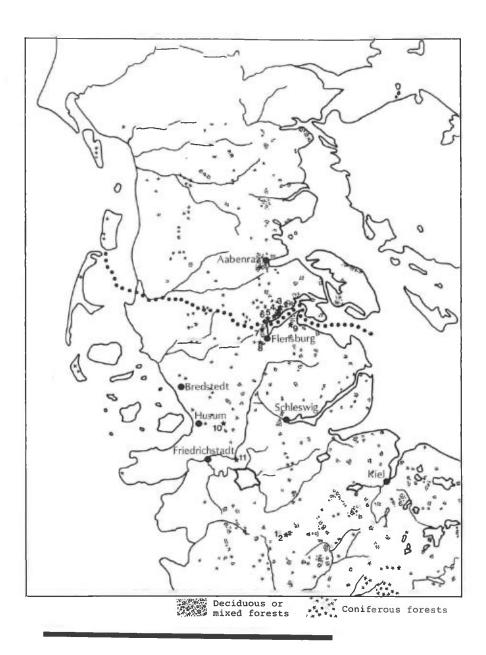


Fig. 1. The known localities of *Triturus alpestris* in South Denmark and in North Germany. The record localities are marked by asterisks with numbers (see text for explanation). The present range of forests (split into deciduous/mixed forests and coniferous forests) is shown but only south of Esbjerg/Kolding and on the adjacent islands (excluding the area of the island Funen). Major towns are shown (marked by big dots). The line of dots represents the Danish/German border. Bar represents 100km.

physiography of the area, the former dispersal towards north is discussed. The migration to the breeding pond is compared with that of Central Germany.

METHODS

In Southeast Jutland ponds have been investigated, primarily to ascertain the presence of *T. alpestris*. For the mapping survey the existence of larvae is given highest priority because it demonstrates a breeding success, not just a possibly accidental presence of single newts.

To explain the current Danish range of *T. alpestris*a reconstruction of the forested areas of southern Jutland and northern Germany at around years 1649-1652 has been made, based on Johannes Mejer's maps (Nørlund, 1942; Domeier & Haack, 1963).

For a comparison of the migration date to the breeding pond (i.e., the date when the newts enter the banks of the pond), the results of two previously published investigations from Åbenrå (Bisgaard et al., 1979a, 1980) and Central Germany (Blab & Blab, 1981) have been used. The average calendar day has been applied, following Blab & Blab (1981).

RESULTS

1. Distribution

The currently known range of *T. alpestris* in Denmark consists of the area immediately west, southwest and south of Åbenrå and more recent records have been made even south of this area close to the German border (Bisgaard, 1982). More detailed we have so far observed *T. alpestris* in the following Danish areas which are shown in Fig. 1 as areas 1-6.

- 1 West, southwest and south of Åbenrå
- 2 Holbøl Skov
- 3 Kelstrup Skov
- 4 Hønsnap Skov
- 5 Kollund-østerskov (Dyrehave)
- 6 Kollund Skov

The Danish word "skov" means "forest" or "wood".

By the end of 1992 we have recorded the species in a total of 120 ponds in Denmark. We know positively that it has disappeared from 10 ponds which have been filled in or have dried up. Since the individual ponds are not surveyed every year, *T. alpestris* may have disappeared from a few ponds due to a lack of restoration.

The main distribution is in the Åbenrå area where we have recorded *T. alpestris* in 94 ponds, but 7 of them do not exist any more. Here its range covers approx. 9 km² of forests and some fields close to the forests (see "2. Habitat"). They border directly on the town of Åbenrå and comprise the following forest parts, with the number of existing ponds with *T. alpestris* mentioned as well (in total 87 ponds in the Åbenrå area); they have been mentioned in the order from northwest to southeast:

Rise Skov: 2 pondsLindbjerg Skov: 1 pond

- Søst Skov: 6 ponds

- Vestermark (inclusive of Nørre Hesselmark, Enemark, Møllekær, Kogang and Salbjerg): 6 ponds
- Sønderskov: 3 ponds
 Nyværk Skov: 5 ponds
 Årslev Skov: 15 ponds
 Røllum Skov: 15 ponds
- Nybøl Skov: 3 ponds

Røllum Nørremark: 9 ponds
Bolderslev Skov: 8 ponds
Årup Skov: 8 ponds
Stubbæk Skov: 6 ponds

We have been unable to find it in the forest parts named Nørreskov and Jørgensgård Skov, just north and northeast of Åbenrå.

In the smaller South Danish region (areas 2-6) we have recorded *T. alpestris* in 23 existing ponds as follows, listed from north to south (additionally 3 ponds in Kollund Skov have been filled in):

Holbøl Skov: 1 pond
Kelstrup Skov: 6 ponds
Hønsnap Skov: 10 ponds
Kollund-østerskov: 3 ponds
Kollund Skov: 3 ponds

The locality record in Holbøl Skov forms the newest known area. For the first time we found *T. alpestris* larvae in September 1991 (with confirmed records during the autumn 1992).

Holbøl Skov, Kelstrup Skov and Hønsnap Skov are in direct contact and form one piece of forest. Kollund-østerskov and Kollund Skov are isolated units, separated by fields and human habitations (300m between Hønsnap Skov and Kollund-østerskov, 2500m between Kollund-østerskov and Kollund Skov).

Out of the 110 existing ponds where *T. alpestris* has been registered, 37 have been created since 1980 (21 or which have been created since 1989) and subsequently colonised. We have never moved newts from one locality to another; they are released in the same pond immediately after capture and identification.

Opposite to the Danish areas nos. 2-6, on the German side of the Inlet of Flensburg the species has been recorded in a small ditch-like water body in the area of Glücksburg (no. 9 in Fig. 1) by Thomas Jarstorff, Flensburg (Bisgaard, pers. comm. 1988); on 26 October 1982 he reported it (verified by a photograph) to Bisgaard and said that it had been found there "recently" (i.e., presumably not more than 5-10 years before that date). Moreover, it is known from a few localities in the area of Flensburg (nos. 7-8 in Fig.1) (Dierking-Westphal, 1982), however, according to Bisgaard (pers. comm. 1988) breeding ponds have been lost there after the construction of a motorway. From the Danish-German border region the next known localities towards south are the area of Husum/Schwabstedt/Friedrichstadt (nos.10-11) (Jaeckel, 1954; Dierking-Westphal,

1982). Locality no. 12 is on the moors of Itzehoe near Hohenwestedt (Dierking-Westphal, 1982).

There are some gaps between the above localities: 14km between the range near Åbenrå (Stubbæk Skov) and Holbøl Skov, and approx. 40km between Flensburg and Husum/Schwabstedt.

2. Habitat

All Danish records of *T. alpestris* have been made in ponds in connection with deciduous forests or more rarely mixed forests. The 120 known ponds (including the 10 which do not exist any more) have been situated inside forests (59 ponds - 49%), on the edge of forests (46 ponds - 38%) or in the open land close to forests (15 ponds - 13%). Out of the 32 ponds which have been created since 1980, 19 (60%) are inside forests, 16 (43%) on the edge of forests and 2 (5%) in the open land.

The ponds in the open land are located up to 80m away from the forest edge; in such cases the surrounding fields consist of pastures for cattle or uncultivated fields rather than arable fields.

The ponds have a surface of less than 200m^2 , but one water body (a small forest lake) with an existing population in Kollund-Østerskov is bigger, \emptyset - 30m, with an island in the middle, \emptyset - ca. 5m.

Inside forests it may sometimes be found even in shaded ponds without vegetation; at rare occasions we have recorded adults as well as larvae in such ponds. Otherwise there is usually a rich growth of for instance floating sweet-grass (Glyceria fluitans), broad-leaved pondweed (Potamogeton natans), common water-plantain (Alisma plantago-aquatica), water starworts (Callitriche spp.), Canadian waterweed (Elodea canadensis), common water crawfoot (Batrachium aquatile [- Ranunculus aquatilis]), branched bur-reed (Sparganium erectum), common duckweed (Lemna minor), great duckweed (Lemna [- Spirodela] polyrhiza) and more rarely brooklime (Veronica beccabunga), stonewort (Chara spp.), willow moss (Fontinalis antipyretica) and common reed (Phragmites australis).

The following trees and shrubs are most frequently found growing near or even in the breeding ponds of *T. alpestris*: common alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*), sycamore (*Acer pseudoplatanus*), beech (*Fagus silvatica*), hornbeam (*Carpinus betulus*), oak (*Quercus robur*), hawthorn (*Cratoegus laevigata*), blackthorn (*Prunus spinosa*), dog rose (*Rosa canina*) and hazel (*Corylus avellana*).

One pond with *T. alpestris* in Kollund Skov is entirely surrounded by the Norway spruce (*Picea abies*), but it is situated just 20m from the deciduous forest. The pond was established in 1989 and the spruces are still fairly small, allowing other vegetation on the forest floor and in the pond. The spruces are believed to have been planted in 1987.

Commonly *T. alpestris* co-exists with the two other species of newts, *T. vulgaris* and *T. cristatus* (Bisgaard et al., 1980). Anurans which we have found in the breeding ponds of *T. alpestris* are *Bufo bufo*, *Rana arvalis* and *R. temporaria*. Only in one case we have found a *Natrix natrix* in a pond with *T. alpestris*.

DISCUSSION

1. Distribution

The number of registered Danish ponds inhabited by *T. alpestris* has increased steadily since 1975. In 1975 it was known from 5 ponds, in 1976 from 17 ponds, and in 1977 and 1978 from 34 ponds (all in the Åbenrå area) one of which was eliminated by draining in 1977 (Bisgaard et al., 1979a). During the past 14 years to 1992 the number of existing ponds with *T. alpestris* has been tripled, from 33 to 110 ponds. With the inclusion of destroyed *T. alpestris* ponds more than the increase is even bigger, from 34 to 120 ponds. The knowledge of its presence in the southeasternmost part of Jutland is newer as it was reported by Bisgaard (1982) from 7 ponds, 4 of which still exist. Today it has in that part been recorded in totally 26 ponds, of which 23 ponds still exist.

The marked increases in the known number of *T. alpestris* ponds are the result of creation of new ponds (37 with *T. alpestris* since 1980) and restoration of existing ones as well as improved surveys of the forests and ponds.

There are some gaps in the distribution shown in Fig. 1. The distance between the area near Åbenrå and Holbøl Skov (areas 1 and 2) is 14km; and it is approx. 40km between Flensburg and Husum/Schwabstedt (areas 8 and 10). We have successfully checked ponds between Åbenrå and Holbøl Skov although small populations may still exist in the interjacent forests. According to Dierking-Westphal (1982) T. alpestris is rare and threatened in Schleswig-Holstein, North Germany, but we are not aware how intensively Schleswig-Holstein has been investigated. Some populations of T. alpestris may well be overlooked in general mapping surveys of a major area like Schleswig-Holstein.

The gap in the Danish distribution (14 km) is minimal. Considering that North Germany perhaps needs to be surveyed in more detail, the gap of 40 km may not necessarily reflect the current extent of fragmentation of the range. Also for the reasons mentioned below (see "3. Dispersal") the northern distribution of *T. alpestris* is likely to have been continuous in historical times.

An extensive mapping survey of the amphibians and reptiles in the whole of Denmark has been carried out, with contributions from many persons. No records of *T. alpestris* have been made outside the range reported here, neither in ponds in/near forests nor elsewhere. The results of the survey are now being prepared for publication by the coordinator Kåre Fog.

2. Habitat

The preference for forested country is in accordance with other observations made in Central European lowland populations (Blab et al., 1976; De Fonseca, 1980; Feldman & Belz, 1981; Parent, 1984; Bergmans & Zuiderwijk, 1986; Bauer, 1987; Glaw & Schütz, 1988). The land habitat selection shows a strong and consistent connection to deciduous forests in Denmark and presumably also in North Germany (Dierking-Westphal, 1982). But apparently the connection is not so consistent throughout the Central European lowlands. Particularly Bergmans & Zuiderwijk (1986) report a substantial portion of the Dutch breeding ponds away from forests; 65% in direct association with forests, 12% less than 150m from forests and 23% more than 150m away from forests (n-165).



Plate 1. Cattle pond with *Triturus alpestris*, *T. vulgaris* and *Rana arvalis* on the edge of the forest, Årslev Skov, near Åbenrå (area 1). The main vegetation consists of floating sweet-grass (*Glyceria fluitans*), broad-leaved pondweed (*Potamogeton natans*) and common duckweed (*Lemna minor*). Photo taken on 22 April 1989.



Plate 2. Shallow forest pond with *Triturus alpestris* inside Kelstrup Skov in the South Danish area (no. 3), drying up during the late summer. In the pond grows floating sweet-grass (*Glyceria fluitans*) and common duckweed (*Lemna minor*). The dominating vegetation around the pond is beech (*Fagus silvatica*), ash (*Fraxinus excelsior*), holly (*Ilex aquifolium*) and raspberry (*Rubus idaeus*). The pond was dug deeper in October 1990. Photo taken on 23 April 1989.



Plate 3. One pair of Triturus alpestris, from the Åbenrå area.



Plate 4. One larva of *Triturus alpestris*, from the Åbenrå area.

All illustrations, including photos: Henrik Bringsøe.

The split between Danish breeding ponds inside forests (49%), on the edge of forests (38%) and in open fields close to forests (13%) probably says more about the placing of water bodies than about the habitat preference of *T. alpestris*. Traditionally there have been many cattle ponds made by the farmers. Especially since 1989 we have noticed an increase in the number of created and restored ponds arranged by the State Forest Service, in accordance with the new guidelines and recommendations for management of the forests put forward by the Danish conservation authorities (Skov- og Naturstyrelsen, 1989). Most of these newly created ponds have been placed inside forests. Otherwise much restoration of existing and creation of new ponds in privately owned areas (forests as well as fields) have been made and financed by our working group.

Its tolerance to shaded ponds is supported by De Fonseca (1980), Bergmans & Zuiderwijk (1986), Blab (1986), Bauer (1987) and Glaw & Schütz (1988), stressing the few and limited requirements to the water habitat.

3. Dispersal

The thermal requirements of *T. alpestris* are similar to those of *T. vulgaris* and *T. cristatus* (Blab, 1986), however, its northern limit is situated more than 1100km further south than those of *T. vulgaris* and *T. cristatus*. The only significant difference in habitat selection which we have observed is that *T. alpestris* has in Denmark so far always been found in connection with deciduous forests. *T. vulgaris* is often found away from forested land and to a lesser extent this also applies for *T. cristatus*.

Its association with deciduous forests suggests that the open land today forms a barrier which prevents *T. alpestris* from dispersing to suitable habitats in other parts of Denmark.

Up to the Palaeolithic and Mesolithic Stone Ages (year 4000 B.P.) Denmark was covered by forests; during the Neolithic Stone Age (year 4000-1800 B.P.) still the vast majority of Denmark was covered by forests. Fields and commons for grazing were present at the time of the Early Bronze Age (year 1800-1000 B.P.), and the first small areas of heath were formed. Through the Iron Age (from year 500 B.P.) and the Middle Ages clearing of forests throughout Denmark and the increasing range of the heath in West Jutland and in parts of Central Jutland continued gradually. However, during these periods deciduous forests were still the predominant vegetation type. Clearings and open farmland still had a limited extent. Only during the latest two to four centuries the reduction of forests through the establishment of open farmland might have broken the dispersal routes of *T. alpestris* and formed barriers preventing it from dispersing northward from Åbenrå. The above information on the vegetational development has been provided by Aaby (pers. comm., 1989).

Fig. 2 shows a reconstruction of the forested areas of southern Jutland and northern Germany at around years 1649-1652. The distribution map of *T. alpestris* (Fig. 1) shows the present range of forested areas (split into deciduous/mixed forests and coniferous forests), illustrating the drastic decline in forested areas during the past 340 years. In Denmark the forest areas of Figs. 1 and 2 only comprise southern Jutland south of the towns of Esbjerg/Kolding and the adjacent islands. Funen (the major island east of Jutland) and its adjacent islands

have not been covered. Apparently *T. alpestris* underwent in that region major habitat fragmentation and was isolated.

Hence, it is considered most probable that *T. alpestris* has been dispersing towards the north until the relatively recent major anthropogenic influence prevented the further range expansion from Åbenrå northward in Jutland. Also in view of the above-mentioned small distances between the currently known localities, the origin of the Danish populations is likely to be natural and not due to an introduction.

4. Breeding migration

During spring 1978 and 1979 the working group recorded the migrations to one breeding pond by pitfall trapping in the area near Åbenrå, (Bisgaard et al., 1979a, 1980), altitude 66m. In 1978 the first specimens were trapped on 14 March, the last on 7 April. There was a slight difference in time of migration between the two sexes: on an average of entered the pond 2 days earlier than qq (Tab. 1). The spring of 1979 was extremely cold and the migration was almost one month delayed: the average migration date of 1978 was 25 March whereas that of 1979 was 22 April (tab. 1).

Blab & Blab (1981) also recorded breeding migration of *T. alpestris* in 1978 and 1979; these studies were carried out southwest of Bonn (altitude 170m) in Central Germany, i.e., ca. 500km south of Åbenrå. In 1978 they found an average migration date being 11 days (of 13 days, QQ 7 days) earlier than that of the Åbenrå area; in 1979 the average migration date was 22 days (of 22 days, QQ 21 days) earlier than that of the Åbenrå area (tab. 1). The figures of 1978 are considered representative as the climate of the spring 1978 was quite normal; this is also the case for Bonn (Blab & Blab, 1981). For the comparisons between the migration dates in Åbenrå and in Bonn only average dates have been used since the number of observations was considerably higher in Bonn wherefore the time span was greater.

Table 1
Migration of Triturus alpestris to breeding pond southwest of Åbenrå, South Denmark (altitude 66 m) and southwest of Bonn, Central Germany (altitude 170 m).

		Åbenrå				Bonn		Difference
		n	First	Last	x	n	x	x
	ರೆರೆ	25	14.3	.7.4	24.3	204	11.3	13 days
1978	22	21	14.3	5.4	26.3	105	19.3	7 days
	Total	46	14.3	7.4	25.3	309	14.3	11 days
	ර්ර්	20	30.3	10.5	17.4	182	26.3	22 days
1979	99	25	6.4	10.5	25.4	176	4.4	21 days
	Total	45	30.3	10.5	22.4	358	31.3	22 days
		1						

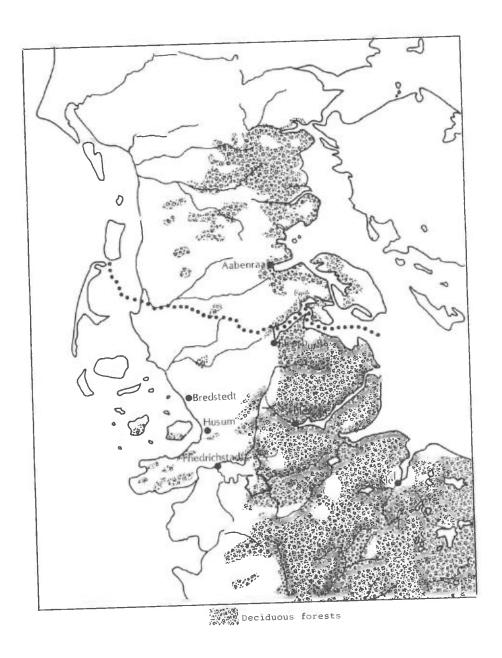


Fig. 2. Reconstruction of the forested areas at around years 1649-52 on the basis of Johannes Mejer's maps. As in fig. 1 only the area south of Esbjerg/Kolding has been considered relevant. The island of Funen and the islands adjacent to Funen have been excluded. Bar represents 100km.

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