



Amphibians and reptiles in North Sweden: distribution, habitat affinities, and abundance (Classes: Amphibia and Reptilia)

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Abstract

North Sweden ('*Norrland*' in Swedish) covers 243 000 km² and lies mainly in the boreal biome. The herpetofauna comprises five amphibian and four reptile species: *Lissotriton vulgaris*, *Triturus cristatus*, *Bufo bufo*, *Rana temporaria*, *Rana arvalis*, *Zootoca vivipara*, *Anguis fragilis*, *Natrix natrix*, and *Vipera berus*.

Successful conservation and management of amphibians and reptiles depend on accurate information about distribution, habitat affinities, and abundance. Such knowledge is also essential as a benchmark to assess changes in distribution and abundance that may come about as a result of climate change and human habitat alteration.

This paper aims to present accurate distribution maps, describe habitat affinities, and provide abundance estimates for the herpetofauna of North Sweden for the period 1970–2022. Distribution data are presented by traditional faunistic provinces, as well as by biotic regions and alpine life zones. Separate sections address post-glacial colonization and a herpetological perspective on anthropogenic changes in relation to species' present status.

Bufo bufo, *Rana temporaria*, *Rana arvalis*, *Zootoca vivipara*, and *Vipera berus* are widely distributed throughout the boreal sub-regions. *Rana temporaria*, *Zootoca vivipara*, and *Vipera berus* also extend into the alpine region. *Triturus cristatus*, *Anguis fragilis*, and *Natrix natrix* occur mainly in the coastal parts of the Southern Boreal region. There are no signs of recent changes in distribution range, but *Lissotriton vulgaris*, *Triturus cristatus*, and *Rana arvalis* have been largely overlooked in the past and have a much wider occurrence than previously recognized. Most species are found in habitats usually not described in all-European field guides. Nearly all anurans hibernate in water. Abundance estimates suggest that some species are more common in the boreal than thought, supporting the notion that a large share of their total European population occurs there. Although local extinctions and declines are known, there are no signs of widespread population decline for any species during the study period.

Key words: boreal, alpine, biotic region, faunistic province, hibernation, newt, frog, toad, lizard, snake

Introduction

North Sweden ('*Norrland*' in Swedish) is a geographic entity embracing the northern 60% of Sweden (Figure 1). Covering an area of 243 000 km², North Sweden is larger than the United Kingdom or Romania, and three times the size of Czechia. Over this vast area, biotic conditions range from pockets of broadleaved hardwood forest in the extreme south to barren alpine heaths in the Scandic Mountain range (the Scandes), and gently rolling subarctic landscapes with scattered dwarfed trees in the extreme north.

The extant herpetofauna of North Sweden comprises five amphibian and four reptile species. None is endemic to the area, and all are widespread elsewhere in Europe.

In North Sweden and beyond, successful conservation and management of amphibians and reptiles depend on accurate information about distribution, habitat affinities, and abundance. Such knowledge is also essential as a benchmark to assess changes in distribution and abundance that may come about as a result of future human habitat alteration and climate change. Several climate model projections for the present century indicate that boreal areas, not least their wetlands, will be subject to more and faster change than habitats in adjacent biomes (Riordan *et al.* 2006; Ruckstuhl *et al.* 2008; IPCC 2018).

Most reference sources on European amphibians and reptiles depict species' distributions in North Sweden

inaccurately. This is true for all major field guides, including recent ones (e.g., Arnold & Ovenden 2002; Glandt 2010; Speybroeck *et al.* 2016), in which the shown range often deviates significantly from the true. In some cases, this deviation amounts to an area equivalent to two Netherlands or more (e.g., *Rana temporaria* in the latter reference). The situation is similar in the European mapping project carried out by Gasc *et al.* (1997). In this atlas, based on a grid of 50 x 50 km squares, a multitude of relevant information is missing from North Sweden (cf. maps for *Rana temporaria*, *Zootoca vivipara*, and *Vipera berus*, which are just as widespread in North Sweden as they are in North Finland). Also, more analytical approaches, such as the composite biodiversity maps in Sillero *et al.* (2014) are based on erroneous and incomplete distribution data when it comes to North Sweden.

Further, information about habitat affinity, abundance, and altitudinal range in the boreal is entirely lacking in most European reference works. This, too, is unfortunate, as in some species a very large share of the total European population *de facto* occurs in habitats not mentioned in current field guides, which instead focus on conditions in Central and Southern Europe. Moreover, hibernation habits of some species are different in the boreal from what is the norm in Central Europe.

Finally, although North Sweden is by no means pristine, its herpetofauna has not been subjected to range fragmentation, habitat loss, and pollution nearly as much as in southern Sweden and Central Europe, where the history of landscape transformation is longer and more profound. Population trajectories and conservation priorities in the latter areas thus need to be complemented by a boreal perspective.

The shortcomings listed above are not altogether due to a lack of knowledge, but mainly because most faunistic and ecological information about amphibians and reptiles in North Sweden has been published in Swedish (e.g., Elmberg 1995 and references therein). There has not been any comprehensive treatment in English of distribution and habitat affinities of the Swedish herpetofauna since Gislén & Kauri (1959), a source that lacks much detail about North Sweden, and one that is obviously outdated. In contrast, more recent information about distribution and abundance of the herpetofauna in neighboring Finland has been available in English for a long time (Terhivuo 1981; 1993).

Given these concerns for inaccurate and missing information about amphibians and reptiles in North Sweden, the objectives of this paper are to present: 1) accurate descriptions of species' distributions in text and maps, 2) information about habitat affinities over the annual cycle, and 3) abundance estimates, for amphibians and reptiles in North Sweden.

Methods

Study area and definitions of geography and biogeography. North Sweden spans a latitudinal range from 60°13'N to 69°04'N and a longitudinal range from 11°58'E to 24°08'E. The border with Norway in the Scandic Mountain range roughly tracks the divide between the hydrological basins emptying into the Atlantic and the Baltic.

Since the days of Carl von Linneaus in the 1700's, faunistic information in Sweden is labeled, organized, and presented by province ('*landskap*' in Swedish; Figure 1). According to the same geographic nomenclature and convention, the vast province of Lapland is further subdivided into five faunistic provinces ('*lappmarker*'; Figure 1). In most cases these traditional provinces differ significantly in extent and borders from the present-day administrative units, the counties ('*län*').

Most of North Sweden is boreal forest (63% of the area below the alpine tree line), abundantly intermixed with open mires (19%) and lakes (11%) (Riksskogstaxeringen 2015–2019). At present a mere 1.5 % is classified as agricultural land (crop field and pasture), but this area was significantly larger in 1850–1950. Agriculture is concentrated on the more fertile soils in river valleys and to coastal lowlands in the east. By European standards North Sweden is sparsely populated.

North Sweden embraces several internationally recognized biotic regions, which are defined mainly by vegetation and climate (Figure 1). From south to north, they are the Boreo-Nemoral, the Southern Boreal, the Middle Boreal, the Northern Boreal, and the Alpine (as adopted in Figure 13 in Hallanaro & Pylvänäinen 2002). The Boreo-Nemoral region (= 'Hemi-Boreal') is represented by pockets in the southernmost province Gästrikland only, and due to their very small area this biotic region is not treated separately in this paper.

The Alpine region begins at the upper limit of the Northern Boreal region (where coniferous forest ends). Due to its wide altitudinal range and large variation in abiotic and biotic conditions, the Alpine region is sub-divided into four life zones (Rune 1965): 1) the Subalpine (lowest), mainly comprising forest dominated by *Betula pubescens*

with other deciduous trees mixed in (*Sorbus aucuparia*, *Prunus padus*, *Populus tremula*, *Salix caprea*), 2) the Low-Alpine, open heath-like habitats above treeline, dominated by bushy willows, grasses and perennial Ericaceae species (heather family), 3) the Mid-Alpine, where low vegetation of stunted willows and Ericaceae is broken up by large areas of mosses, bare ground, and late-lying snow patches, and 4) the High-Alpine, which is only partly vegetated (mainly lichens and mosses) and largely made up by bare ground, rocks and snow patches. The High-Alpine zone does not host any amphibians or reptiles, and it is not treated in this paper. The three lower alpine zones each embrace 200–400 m in altitude. Note that the Arctic biome proper does not range into North Sweden, although some areas in the far north approach such conditions (long cold winters, low precipitation, and small patches of permafrost).

The above terms of biotic regions and alpine life zones are used in this paper when describing range, abundance, and habitat affinities of amphibians and reptiles. Biotic regions and alpine life zones are nouns spelled with capital first letters (e.g., Northern Boreal and Low-Alpine) to distinguish them from the adjectives (e.g., northern, boreal, alpine).

Species included. This paper treats the nine extant species of amphibians and reptiles in North Sweden: Smooth Newt *Lissotriton vulgaris* (Linnaeus), Great Crested Newt *Triturus cristatus* (Laurenti), Common Toad *Bufo bufo* (Linnaeus), Common Frog *Rana temporaria* (Linnaeus), Moor Frog *Rana arvalis* Nilsson, Viviparous Lizard *Zootoca vivipara* (Jacquin), Slow Worm *Anguis fragilis* Linnaeus, Grass Snake *Natrix natrix* (Linnaeus), and Adder *Vipera berus* (Linnaeus). The taxonomy follows Speybroeck *et al.* (2020). Three further species were considered for inclusion:

The Pool Frog *Pelophylax lessonae* (Camerano) occurs in some 120 coastal localities in the neighboring province Uppland to the south. Records have been made E of Skutskär, a mere 4 km from the SE border of Gästrikland (North Sweden) (Swedish Species Observation System, <https://www.artportalen.se/>). *Pelophylax lessonae* in Uppland are dispersive as an adaptation to the gradual natural deterioration of breeding sites, that is, the succession of the latter from open sun-exposed near-sea ponds to shaded forest bogs, a process driven by land uplift due to post-glacial geostatic rebound. Accordingly, this species is a likely future addition to the herpetofauna of North Sweden. This proposition is supported by the recent and unexpected discovery of the taxon in SW Finland (Hoogesteger *et al.* 2013).

The Sand Lizard *Lacerta agilis* Linnaeus occurs in a few relict populations in the adjacent province Dalarna, the closest of which is some 30 km W of the border with Hälsingland (North Sweden). All northern relict populations of this species in Sweden are confined to landscapes with open pine forest and long-term continuity of sun-exposed dune habitat. As areas fulfilling these criteria also occur in North Sweden, the County Administrative Board of Gävleborg (provinces Gästrikland and Hälsingland) surveyed all open dune areas in the county in 2001, but no *Lacerta agilis* were found (Andersson & Berglind 2003). There is a published record from between Gävle and Bönan (Gästrikland) around 1880 (Olsson 1882). No specimen was collected at that time, though, and none were observed when the site was revisited in 2001 (Andersson & Berglind 2003). It seems very unlikely, though not altogether impossible, that *Lacerta agilis* occurs in undiscovered isolated relict populations somewhere in southernmost North Sweden.

The Smooth Snake *Coronella austriaca* Laurenti has been claimed from a few sites in North Sweden (viz. Ångermanland (Ekman 1922) and Medelpad (Gylling 1898)). However, none of these early reports was verified by collected specimens or a detailed description. A report from Njutånger, Hälsingland (Hanström 1958) includes a fairly accurate description, but there is not any documentation, and confusion with an aberrant *Vipera berus* cannot be ruled out. The closest known present-day occurrences of *Coronella austriaca* are in Uppland, some 110 km SE of the southern border of North Sweden (Gästrikland). The species cannot be regarded as part of the present herpetofauna of North Sweden, and it is doubtful that it has ever occurred here.

The only records of alien amphibians and reptiles in North Sweden concern *Trachemys scripta* (Thunberg) (Pond Slider, native of eastern USA) and were made in 2021: Härnösand (Ångermanland) and Gävle (Gästrikland)(www.artportalen.se). These two turtles were obviously released pets with very limited survival possibilities.

Data sources for distribution maps. The distribution maps presented here are based on records 1970–2022. This may be seen as an overly long time window but restricting maps to records from the last 10–20 years would create a problem, as North Sweden has few explorative herpetologists and maps based on recent data only would exclude too much relevant range information. Further, there is little evidence that land use change and other anthropogenic impact have led to significant range changes during this period (cf. species accounts below).

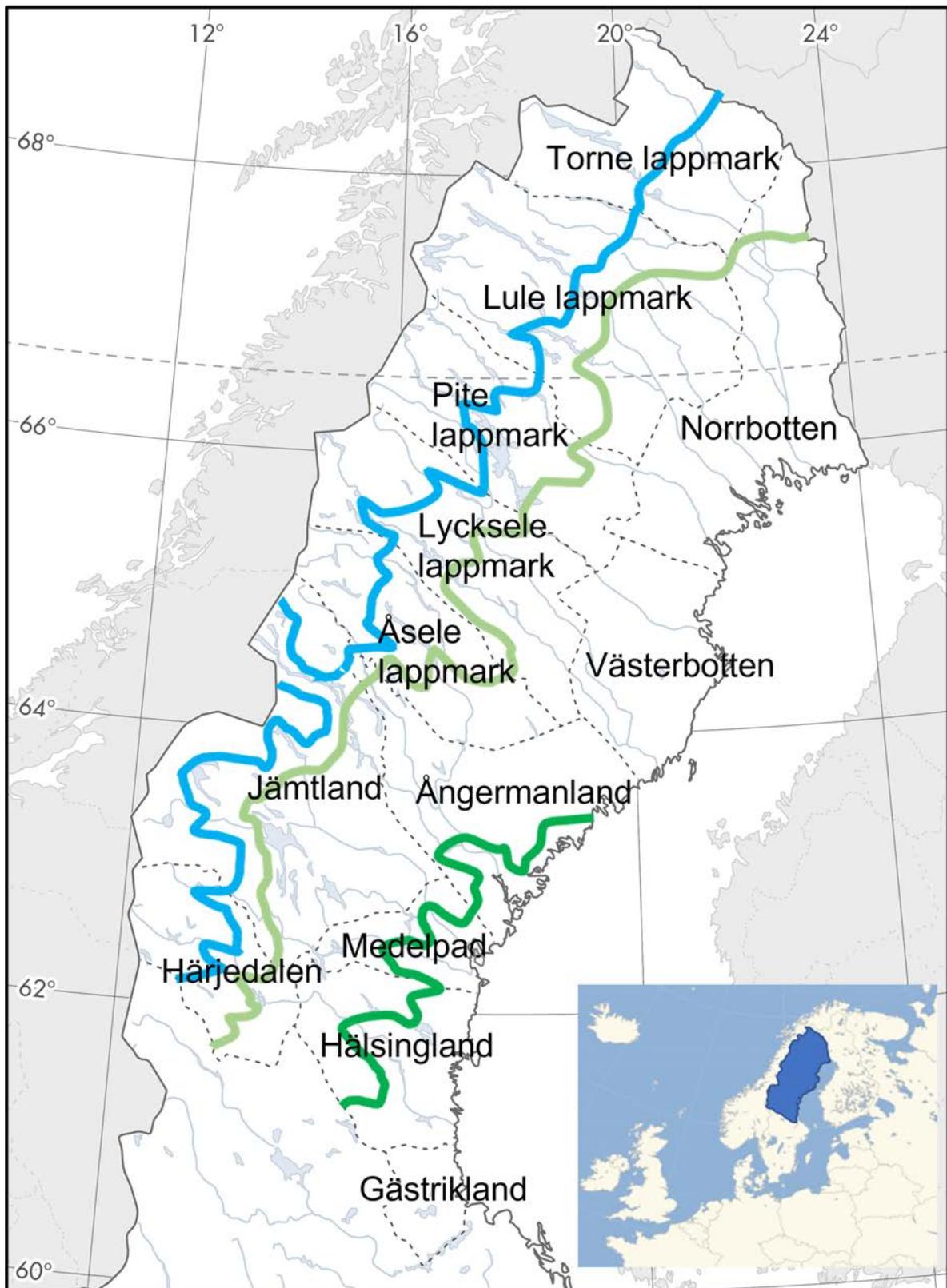


FIGURE 1. Faunistic provinces in North Sweden and their names. Dashed lines are borders between provinces and solid lines inland show the national borders with Norway (west) and Finland (east). Areas southeast of the dark green line are in the Southern Boreal biotic region. Areas between the dark green and light green lines are in the Middle Boreal biotic region. Areas between the light green and blue lines are in the Northern Boreal biotic region. Areas west and northwest of the blue line are in the Alpine biotic region, which is further subdivided into life zones based on altitude (see Methods). Map template by Nils Wallin, Kristianstad University. Inset map shows location and extent of North Sweden in Europe.

Distribution maps were based on four primary sources: 1) records and maps in Elmberg (1995), a source that also contains a fairly complete bibliography of older published primary distribution data (mainly in Swedish), 2) unpublished records post-1995 made by me and trusted fellow herpetologists, 3) published organized surveys, mainly by County Administrative Boards (cited in species accounts, when applicable), and 4) reports in *Artportalen*, a national web-based species reporting platform for the public (<https://www.artportalen.se/>, last accessed February 7th, 2023). As in any citizen science project, data quality is sometimes a problem in the *Artportalen* observation system. For example, many pictures uploaded to document reports of *Rana arvalis* actually show *Rana temporaria*. To safeguard data quality as far as possible I used species-specific selection criteria when including records from *Artportalen* in the distribution maps in this paper. These criteria are described in each species account below, and the resulting final number of included records from this source is given. Inevitably, this procedure excludes some accurate records, but I do not see that as changing the general picture of any species' range.

In some species accounts distribution and records pre-1970 are mentioned briefly to complement the present situation, but those interested in the historical distribution should consult Gislén & Kauri (1959; in English) and Elmberg (1995; in Swedish).

Data sources for habitat affinity. These texts are mainly based on my own field experience since 1972 and on discussions with fellow herpetologists who have extensive experience from field work in North Sweden (e.g., Stefan Andersson, Stefan Ericsson (deceased), Anders Forsgren, and Mattias Hagman). Note, though, that much information about habitat affinity has previously been published in Swedish (cf. Elmberg 1995 and references therein).

Data sources for abundance estimates. In reptiles, and especially in amphibians, juvenile age classes have much higher mortality rates than do adults, making it relevant to express abundance in terms of individuals in reproductive age. Moreover, it is easier to monitor and estimate numbers of adults than of juveniles, especially anurans as they are conspicuous at breeding sites. Empirical abundance data in this paper come from counts of anurans at breeding sites (calling males, adults of both sexes, and spawn clumps) and of some reptiles after emergence from hibernation sites. In addition, some abundance estimates are given for larger areas in which intensive field work was carried out for several years. All abundance estimates in this paper refer to adults per km².

There are not any data available about population density measured in summer habitats *per se* (cf. Elmberg 2008). This means that abundance estimates for larger areas presented here are based on a combination of extrapolated hard data (mainly from spring counts), my own field experience, and calibration with other field herpetologists active in North Sweden.

I carried out standardized annual counts of calling anurans in spring at ten sites in Umeå (Västerbotten) and Ammarnäs (Lycksele lappmark) in the 1980's (Elmberg, unpublished). Apart from these, there has never been any long-term monitoring programs of amphibians and reptiles in North Sweden. Nevertheless, anecdotal reports and field experience by the author and consulted colleagues suggest some long-term trends post-1970, which are presented in the species accounts.

Post-glacial colonization and zoogeography

Amphibians and reptiles in North Sweden are recent colonists. A massive glacier covered the entire area during the latest glaciation. When it melted 10000 years ago, most of today's coastal lowlands in North Sweden were under the waters of the Baltic. Ever since the glacier's disappearance there has been land uplift, that is, a post-glacial geostatic rebound. This process is ongoing at a rate of up to 1 cm per year. Consequently, new land is continuously rising out of the sea along the coast of North Sweden, gradually forming new islands and transforming bays of brackish water into freshwater lakes, and with time into mires. As a result, the age of coastal lakes and offshore islands can be backdated with fair precision, and their colonization by amphibians and reptiles can be studied in retrospect. Present-day occurrence on offshore islands thus indicates the dispersal capacity of different species.

Although today's coastal lowlands were sea bottom at the time, higher parts of North Sweden early on had land connection to the European continent from the south via southern Sweden and Denmark, and from the east via Finland. In other words, amphibians and reptiles have had two possible immigration routes to North Sweden. Recent methodological advances in genetics provide tools for reconstructing these post-glacial immigration events. Insights about present-day geographical genetic variation have led to description of new and resurrection of previously

surmised distinct taxa (Speybroeck *et al.* 2020). For example, European Slow Worms *Anguis* are now considered as five different species, of which *Anguis fragilis* occurs in North Sweden and *Anguis colchica* on the other side of the Baltic, in Finland. Dual immigration routes to Fennoscandia seem likely also for *Rana arvalis* (Cortazar-Chinarro *et al.* 2018), *Natrix natrix* (Kindler *et al.* 2014), and possibly *Rana temporaria* (Palo *et al.* 2004). At any rate, the time elapsed since North Sweden was colonized appears too short for major regional evolutionary divergence to have arisen in any of the species.

The climatically most benign period for thermophilic ectotherms after the latest glaciation occurred 8000–5000 years before present. The northward expansion of amphibians and reptiles in North Sweden most likely reached its peak during the late part of this period. The same should be true for the altitudinal expansion into the Scandic Mountains. The latter process is less relevant for the immigration of amphibians and reptiles into North Sweden, but more so for possible subsequent dispersal into Norway. In the latter country, there are extant occurrences of *Lissotriton vulgaris* in the provinces ('fylke' in Norwegian) of Sör-Trøndelag, Nord-Trøndelag, and Nordland (www.artskart.artsdatabanken.no). As Gislén & Kauri (1959) proposed, these occurrences are more parsimoniously explained by immigration from Sweden (i.e., present-day Jämtland) rather than by south-to-north dispersal through the very rugged Norwegian terrain.

Starting about 3000 years before present the climatically benign period was followed by a more adverse climate. It is generally believed that the turn to cooler summer conditions led to a gradual range retraction in some species, so that previously continuous distributions were fragmented into remnant local populations in pockets enjoying more favorable local climatic conditions. The present-day patchy occurrence of *Vipera berus* in the Northern Boreal and of *Lissotriton vulgaris* and *Triturus cristatus* in the Middle Boreal of North Sweden all fit well with such a scenario (cf. Gislén & Kauri 1959, p. 233).

Species accounts

The species accounts in this paper have a consistent structure. The first section describes distribution and begins with the criteria for inclusion of reports from *Artportalen* (data source 4 in Methods). Next follow comments to the map for each species (see Methods for time frame and definitions of biotic regions and alpine zones). Then the range of biotic regions and alpine zones of occurrence is described. The highest known altitude in the Alpine region is sometimes given. However, it is generally more relevant to describe altitudinal distribution by Alpine life zone rather than in meters above sea level, as all life zones begin and end at lower altitude with increasing latitude. Next follows text about occurrence patterns on offshore islands along the Baltic coast. Finally, a brief statement is given about any known change in distribution 1970–2022. The occurrence by traditional faunistic provinces is summarized in Table 1. A second section of the species accounts describes habitat affinities, movements in different seasons, and hibernation habits. No attempt is made to list all utilized habitats. Instead, those predominantly used in North Sweden are described. The third section lists any information about abundance estimates and historical trends thereof.

The species accounts focus on conditions in North Sweden and contain much information previously not published in English. Comparison with and references to conditions in neighboring countries have been kept to a minimum and concern boreal examples only.

Smooth Newt *Lissotriton vulgaris* (Linnaeus 1758)

Distribution (Figure 2). Included records from *Artportalen*: all reports (N=670), as there is no confusion species except the much rarer *Triturus cristatus*.

Widely distributed in the Southern Boreal; in a regular sampling grid covering the entire provinces of Gästrikland and Hälsingland, Sterner (2005) found the species in 42% of 111 squares in which randomly selected wetlands (< 1 hectare, presumed free from predatory fish) were investigated. In both these provinces there is a pattern of more widespread occurrence in coastal areas than farther inland. In a similar randomized survey of Medelpad and southern Ångermanland, Olofsson *et al.* (2008) recorded the species in 23% of 155 randomly selected small wetlands. In the southern Middle Boreal this species is seemingly more patchily distributed, especially in the northern parts of the range. There are only two known extant occurrences in the Northern Boreal: Akkan and Abborrberg (4 kms apart in Stensele parish) in Lycksele lappmark (Persbo *et al.* 2006, Anders Forsgren pers. comm.).

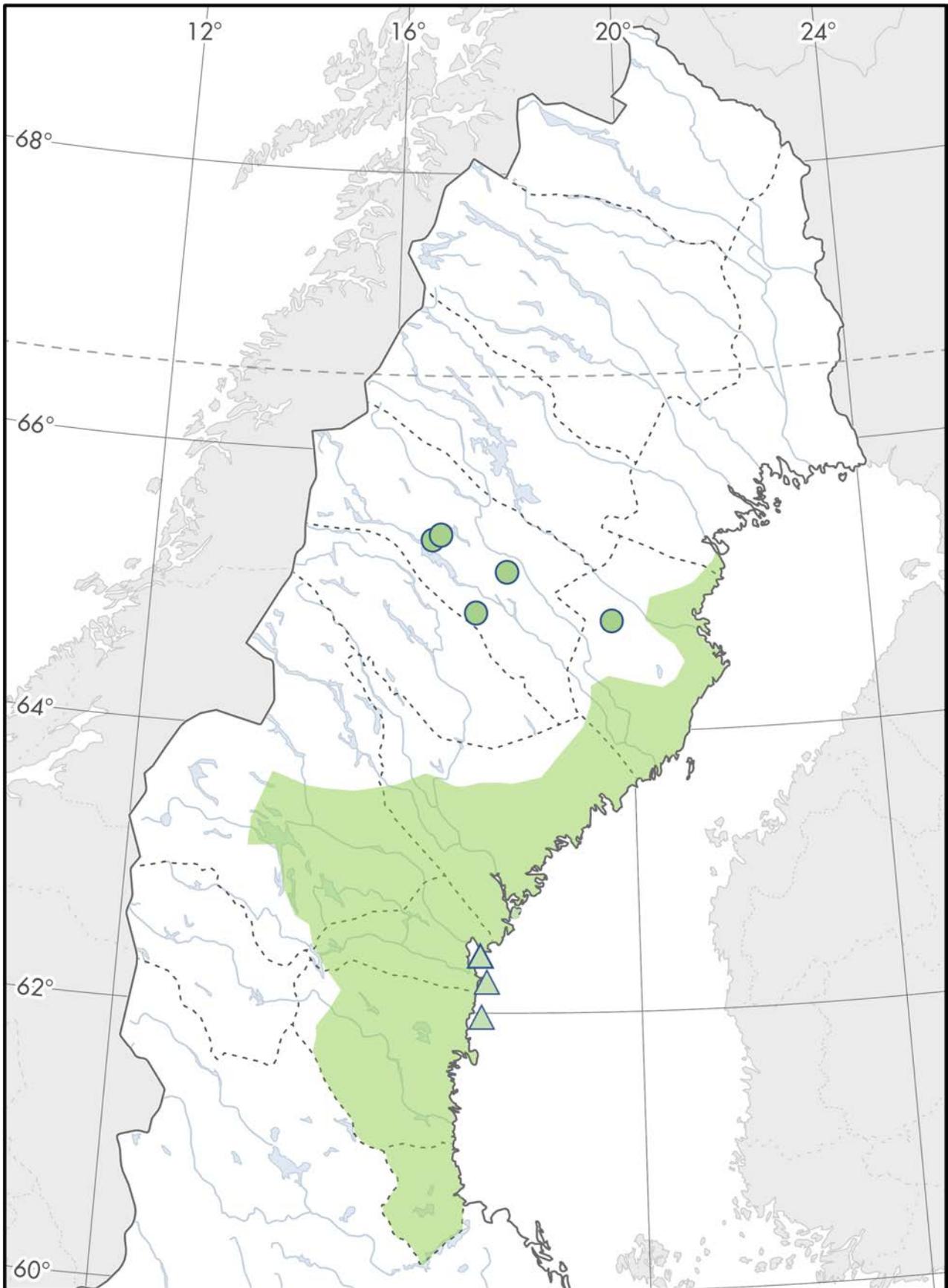


FIGURE 2. Distribution of *Lissotriton vulgaris* in North Sweden. Known continuous range is colored. Possibly disjunct occurrences are denoted by filled circles and offshore records by triangles.

Interestingly, three of the northernmost occurrences are also the highest known from North Sweden (and in Sweden overall): Akkan and Aborrberg are both 520 m above sea level, and Jägarliden at 340 m (all in Lycksele lappmark; Persbo *et al.* 2006).

Offshore occurrence is known from two islands in Medelpad (Brämön and Alnön; Elmberg & Ericsson 1983) and one in Hälsingland (Jättholmarna), indicating a fair dispersal capacity over brackish water. In coastal areas where the species occurs, many mainland records are very close to the sea (Elmberg 1995; Sterner 2005; Persbo *et al.* 2006; Olofsson *et al.* 2008). This pattern indicates a good general dispersal capacity, since such wetlands created by land uplift, are often less than 200 years old.

There are not any data to gauge large-scale changes in distribution during the last 50 years, but local extinctions due to fish introduction have been documented (Dolmen 1978; Elmberg & Ericsson 1983; Persbo *et al.* 2006). One of these populations comprised neotenic individuals only (Långselberget, 460 m altitude, Stensele, Lycksele lappmark; Gislén & Kauri 1959; Dolmen 1978; Elmberg & Ericsson 1983). The northern distribution limit presented here runs farther north than in Gislén & Kauri (1959). This discrepancy is, however, not due to a range expansion but rather because the species has been overlooked before.

Habitat and movements. Breeding habitats include tarns and small lakes in forested areas, as well as more or less permanent man-made wetlands (e.g., ponds, pasture pools, gravel pits). Tarns and lakes are usually oligo- to mesotrophic, bordered either by floating *Sphagnum* mats or by moderately dense stands of aquatic grasses (*Phragmites australis*, *Phalaris arundinacea*) or sedges (*Carex spp.*) (Figure 11). The majority of known breeding wetlands are fishless (cf. Elmberg & Ericsson 1983; Sterner 2005; Persbo *et al.* 2006) and lack connection to other wetlands by streams. Several of the occurrences away from the more continuous range are isolated, either high on forested hills or in large peat bog complexes. Breeding sites are usually permanent wetlands, but the species has been recorded in ephemeral rock pools on the Baltic coast (Elmberg & Ericsson 1983; Aronsson *et al.* 2005; Figure 12).

Summer habits and habitats are little known, as very few observations are made away from the breeding wetlands. Adults can be seen in the latter long into June, sometimes to mid-July. It is thus possible that many remain aquatic for a large part of the summer. During field work at Galtström (Medelpad) August 1st we found active adults on land as well as in a nearby breeding pond. Terrestrial habits in North Sweden are little known; most records on land have been made under logs or woody debris in damp spruce-dominated forest close to breeding sites. Terrestrial summer records have also been made under flat sheltering objects near man-made wetlands.

Hibernation habitats and habits in North Sweden have not been documented; it is not even known whether terrestrial or aquatic hibernation is the rule. However, aquatic hibernation was the only option in the neotenic population at Stensele in Lycksele lappmark, now extinct (Dolmen 1978).

Very little is known about seasonal movements. The almost total lack of observations of adults moving to or from breeding wetlands strongly suggests they spend much of their life in the latter or their close proximity.

Abundance estimates and trends. There are very little data on local abundance, and no indication that any breeding wetland holds more than 200 reproducing adults (e.g., Dolmen 1978; Elmberg & Ericsson 1983; Sterner 2005; Persbo *et al.* 2006; Olofsson *et al.* 2008). Given the patchy distribution, it is unwise to suggest abundance estimates for larger areas. However, the surveys by Sterner (2005) and Olofsson *et al.* (2008), which covered a mere fraction of the suitable wetlands in the Southern Boreal, suggest there must be thousands of breeding wetlands in this region.

There are no indications of changes in abundance over the last 50 years, apart from local extinctions.

Great Crested Newt *Triturus cristatus* (Laurenti 1768)

Distribution (Figure 3). Included records from *Artportalen* (N=320): due to risk of confusion with the more widespread *Lissotriton vulgaris* only records documented by a photograph or made by experienced observers have been included.

Widely distributed in the Southern Boreal; in a regular sampling grid covering the entire provinces of Gästrikland and Hälsingland, Sterner (2005) found the species in 21% of 111 squares in which randomly selected wetlands (< 1 hectare, presumed free from predatory fish) were investigated. It is more evenly distributed in Gästrikland than in Hälsingland, and in both provinces there is a clear pattern of more numerous occurrence in areas near the coast.

In a similar randomized survey of Medelpad and southern Ångermanland, Olofsson *et al.* (2008) recorded the species in 3% of 155 randomly selected small wetlands. In coastal southern Medelpad the occurrence is more or less continuous (Aronsson *et al.* 2005), as it is in coastal Hälsingland and Gästrikland. In the Middle Boreal there are scattered records north to 63°N, most of which from east-central Jämtland. A recent photo-documented record in NE Ångermanland suggests that the species may range further north along the coast than currently known. The only record from the Northern Boreal during the study period is a possibly disjunct occurrence in western Jämtland (Figure 3).

Although most known extant breeding sites are in coastal lowland, at least three are at 300–400 m altitude (Elmberg 1995; Olofsson *et al.* 2008). An extinct population at Långselberget (Lycksele lappmark (Middle Boreal)) was even higher, at 460 m.

Offshore occurrence is known from only one site in North Sweden (Kråkö, Hälsingland). However, several breeding wetlands on the mainland are very near the sea (Sterner 2005; Olofsson *et al.* 2008). This indicates a fair general dispersal capacity, since such wetlands, created by land uplift, are often less than 200 years old.

One local extinction has been documented in the Middle Boreal: the isolated occurrence in Lycksele lappmark, comprising only neotenic individuals, went extinct due to fish introduction in the 1960's (Långselberget, Stensele; Gislén & Kauri 1959; Dolmen 1978; Elmberg & Ericsson 1983). There is not any indication that the general distribution has changed recently in North Sweden. Instead, the species has previously been much overlooked. It is more widespread, more numerous, and the range more extensive to the northwest than depicted in any previous source (cf. Gislén & Kauri 1959; Elmberg 1995).

Habitat and movements. Most known breeding wetlands in North Sweden are small fishless tarns bordered by coniferous forest (e.g., Sterner 2005; Olofsson *et al.* 2008). These wetlands are generally oligotrophic and have floating mats of *Sphagnum* along the shore. However, in coastal areas a fair number of breeding sites of anthropogenic origin are known: farmland ponds, disused fishponds, peat quarries, gravel pits, and golf course ponds. Many of these are meso- to eutrophic and thus more resemble typical breeding habitats in South Sweden. Most known breeding wetlands are permanent, but some are more ephemeral, such as depressions in wet forest and rock pools near the Baltic (Olofsson *et al.* 2008).

Observations of moving or migrating individuals are exceedingly few. Their scarcity and location strongly suggest very limited movements away from breeding wetlands and imply a largely aquatic lifestyle in summer, too.

Summer habitat use is almost unknown; a few records of terrestrial adults have been made, mainly under woody debris or in brooks in old spruce-dominated forest near breeding wetlands. During field work at Galtström (Medelpad) August 1st, we found active adults on land and in a nearby breeding pond, as well as hiding under woody debris in the upper part of the seashore littoral.

Nothing is known about hibernation habits in North Sweden, that is, whether terrestrial or aquatic. However, aquatic hibernation must have been the rule in the extinct neotenic population at Stensele in Lycksele lappmark (Dolmen 1978).

Abundance estimates and trends. There are not any data about local abundance. Given the patchy distribution, suggesting abundance estimates for larger areas is unwise. However, the surveys by Sterner (2005) and Olofsson *et al.* (2008), which covered a mere fraction of the suitable wetlands in the Southern Boreal suggest there must be several hundred breeding wetlands in this region.

There are no indications of changes in abundance over the last 50 years, apart from local extinctions.

Common Toad *Bufo bufo* (Linnaeus 1758)

Distribution (Figure 4). Included records from *Artportalen* (N=1325): all reports have been included from the Southern, Middle, and Northern Boreal. However, in the Alpine region inexperienced observers may confuse this species with locally dark and short-limbed *Rana temporaria*. Therefore, only records of calling males, those made by known experienced observers or documented by pictures have been included from the Alpine region and adjacent uppermost parts of the Northern Boreal.

Widespread and common throughout the Southern and Middle Boreal, scarce but widespread in lower altitudes of the Northern Boreal north to Lule lappmark. The documented northern distribution limit runs near the Arctic Circle but could be farther north (Figure 4).

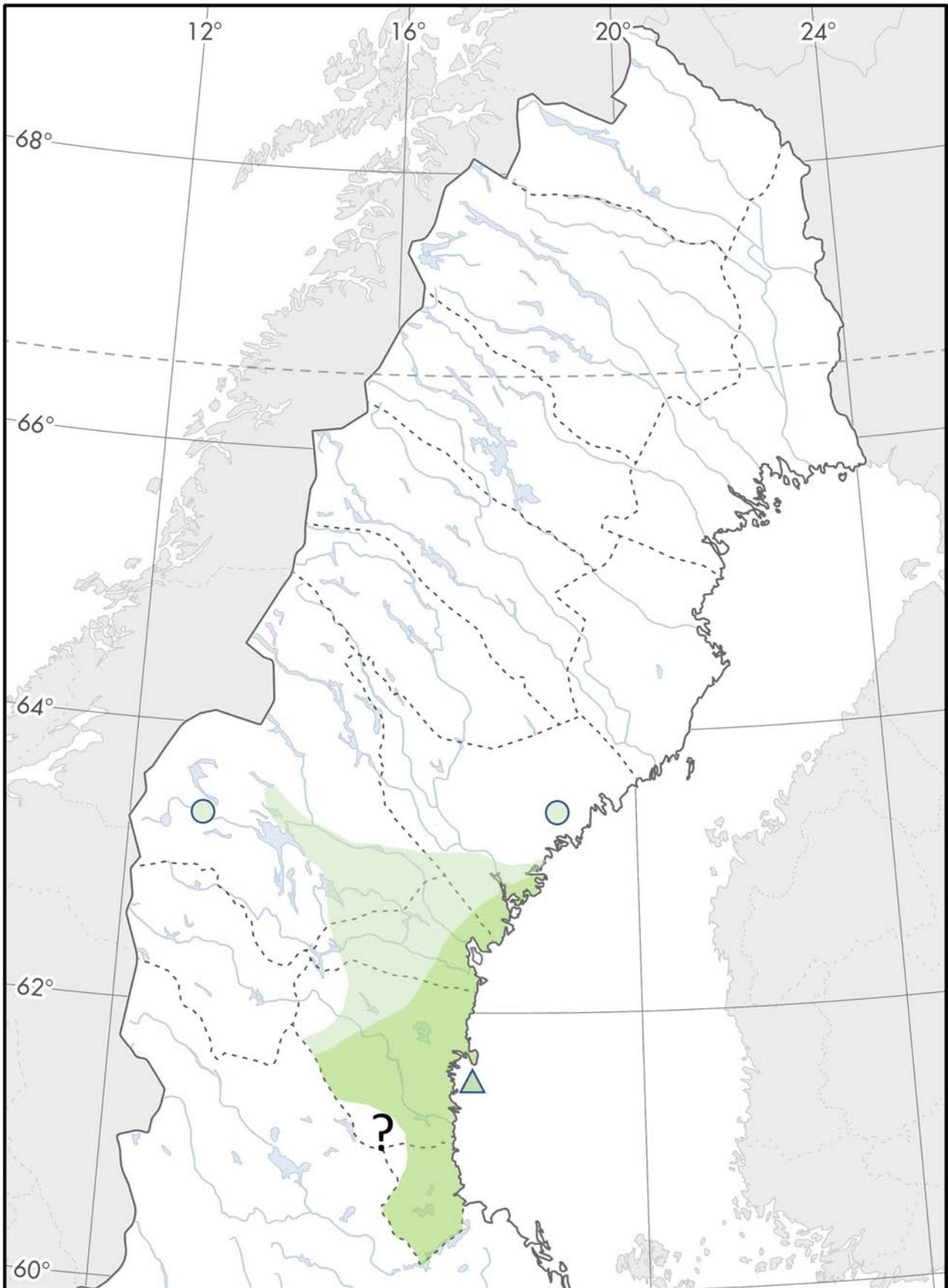


FIGURE 3. Distribution of *Triturus cristatus* in North Sweden. Areas colored darker denote more continuous range, and lighter color areas where records are more scattered. Likely disjunct occurrences are shown by filled circles and an offshore record by a triangle. A question mark shows area where presence is likely but has not been documented.

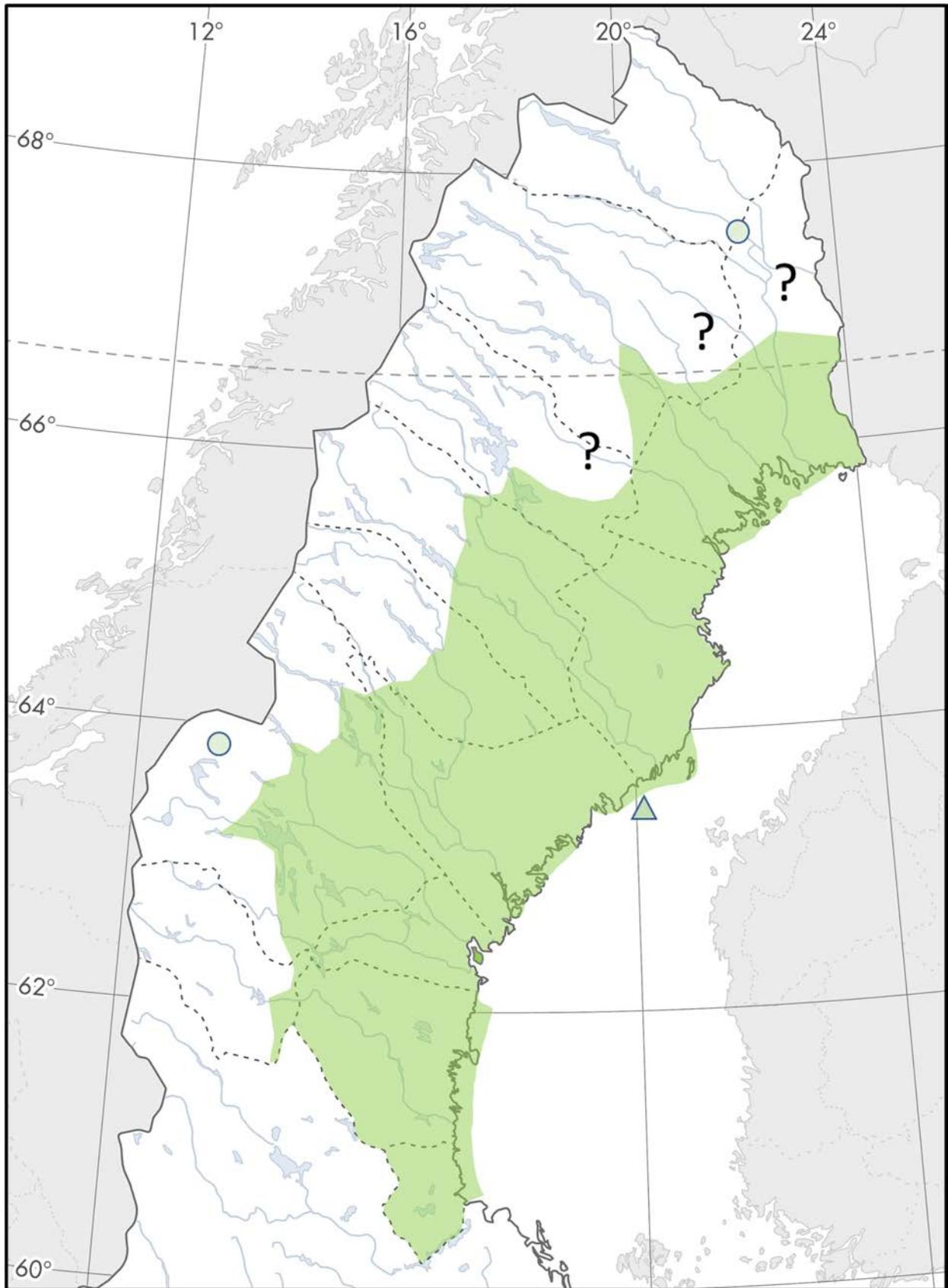


FIGURE 4. Distribution of *Bufo bufo* in North Sweden. Colored areas of the Baltic are those with widespread occurrence on offshore islands. The extremely isolated offshore occurrence on the islet Bonden is shown by a triangle. Possibly disjunct occurrences in northern Norrbotten and close to the Alpine region in Jämtland are shown by a filled circle. Question marks show areas where presence is possible but has not been documented.

As expected, the highest records are from the southern part of the Scandic Mountains (580 m altitude; Tjovre, Jämtland). Farther north, the highest records in Lycksele lappmark are at 475 m, and at 270 m in Lule lappmark, where the northern range limit bends east towards Finland.

Summertime occurrence and reproduction are known from many far offshore islands along parts of North Sweden's coast, indicating a very high dispersal capacity over brackish water. This is the only amphibian known from the tiny and extremely isolated islet Bonden (Ångermanland, 63°25'55.0"N, 20°2'19.4"E; Figure 4), more than 15 km from the mainland.

There are no indications of changes in distribution over the last 50 years. The more extensive occurrence to the north presented here (compared to in Gislén & Kauri 1959) and the first records from Härjedalen do not represent range expansion but are merely due to the species having been overlooked there before. Note, however, that all older and also recently claimed records in the Alpine region (e.g., Holm 1921, Gislén & Kauri 1959; Frislid & Semb-Johansson 1981; *Artportalen*) are likely due to confusion with *Rana temporaria*. Based on current knowledge, the species does not occur in the Alpine region in North Sweden.

Habitat and movements. Breeding habitats include virtually all types and sizes of lakes, tarns, bogs, mires, ponds, and stagnant parts of streams and rivers (Figures 11, 14). The entire range from oligotrophic to eutrophic conditions is utilized, including strongly humic dystrophic wetlands. In barren oligotrophic wetlands, this is the most widespread anuran. As a consequence, it often breeds where there are predatory fish, for example *Perca aquatilis* Linnaeus and *Esox lucius* Linnaeus. Calling males and amplexant pairs are mainly found in nearshore shallow areas with sparse vegetation, but often in more exposed situations than is the case in *Rana arvalis* and *R. temporaria*. Calling males can be observed in rock pools and shallow brackish bays along the Baltic (Elmberg & Ericsson 1982; Figure 12).

After breeding, toads move to summer foraging habitats, which are equally diverse, ranging from dry pine forest, mesic coniferous forest, and lush deciduous bottomland forest to natural grasslands, seashores, meadows, agricultural land, gardens, and parks (Figure 13).

In dry and warm summer weather this is the only amphibian commonly moving around in the open. Movements from summer habitats to hibernation sites can be noticeable on warm damp nights in early autumn but are not as synchronized and spectacular as in the *Rana* species.

Hibernation is usually aquatic, taking place in breeding wetlands or in nearby streams and rivers. Terrestrial hibernation has been documented in the Middle Boreal (Elmberg 1995) but based on current knowledge it must be considered as an exception from the rule. Hibernation in brackish water has been documented from northern Ångermanland (Elmberg & Ericsson 1982).

Abundance estimates and trends. There are not any published data on local abundance, but a large number of roadside surveys of chorusing anurans in Ångermanland and Västerbotten in the 1980's showed that *Bufo bufo* is often less numerous at the wetland level, but more widespread at the landscape level compared to *Rana temporaria* and *R. arvalis*. This difference is largely because it occurs in more truly oligotrophic conditions (Elmberg & Ericsson 1982). Abundance estimates based on extensive field work in the Umeå area (Västerbotten, Middle Boreal) 1975–1994 run in the neighborhood of 400–600 adults/km² in representative landscapes near the coast (Elmberg, unpublished). Lower densities are likely in the Northern Boreal region. There are no indications of changes in abundance over the last 50 years.

Common Frog *Rana temporaria* Linnaeus 1758

Distribution (Figure 5). Included records from *Artportalen* (N=2000): a ubiquitous species for which all reported records have been included. Any rare confusion with *Rana arvalis* would not change the overall picture of distribution or abundance.

Widespread and abundant throughout the Southern Boreal, Middle Boreal, Northern Boreal regions, and in the Subalpine life zone. Widespread and locally common in the Low-Alpine zone. Scattered occurrences in the Mid-Alpine zone (Figures 15, 16).

Breeding sites in the Low-Alpine zone reach at least 840 m altitude in Lycksele lappmark (Elmberg 1991; Figure 17) and probably up to or above 1000 m further south in the Scandic Mountains. In other words, it is a widespread breeder well above treeline. In summertime adults have been observed at 1070 m in Åsele lappmark and Lycksele lappmark, and at up to 1400 m in Jämtland (Helagsfjället), all of which are in the upper part of the Mid-Alpine zone.

Occurrence and reproduction are known from several far offshore islands in the Baltic in the three northernmost coastal provinces (Norrbotten, Västerbotten, and Ångermanland), where distributed offshore equally widely as *Bufo bufo*. In the coastal provinces farther south, however, offshore occurrence is scarcer and concentrated to more nearshore islands. This may indicate a somewhat lower dispersal capacity over brackish water than in *Bufo bufo*.

There are no signs of changes in distribution during the last 50 years.

Habitat and movements. Spring migration of adult males to breeding ponds is largely nocturnal and often strongly synchronized, with up to 50% arriving within a few days (Elmberg 1990). Adult females arrive more gradually to breeding sites (Elmberg 1990). Juveniles emerge later than adults and are rarely seen before the spawning period is over.

Breeding habitats range from ponds and bogs above treeline (Figure 17), through any type of wetland and lake in lower biotic regions, to sheltered shallow brackish bays of the Baltic (Elmberg *et al.* 1979). They further range from wetlands in pristine forest to landfill swamps, flooded disused gravel pits and quarries, and man-made ponds in residential areas. The entire range from the most oligotrophic to the most eutrophic conditions is utilized for breeding (Figures 11, 14). This is the most frequently encountered anuran breeding in barren rock pools along the Baltic seashore (Figure 12). Calling males and spawn clumps are usually found in shallow and well vegetated situations, that is, less exposed than eggs of *Bufo bufo* and *Rana arvalis*. Females remain in breeding wetlands only until they have deposited their eggs, whereas adult males remain as long as there are receptive females around, or longer (Elmberg 1990).

Dispersal from breeding sites to nearby summer foraging habitats is gradual and not very conspicuous. Since *Rana temporaria* is so widespread and abundant, summer foraging habitats are extremely diverse, from alpine heath, open coniferous forest to dense bottomland woods along the major rivers (Figures 15, 18). The highest summer densities are observed in abandoned fields and grassy meadows along lakes, rivers, and seashore, but also in deciduous forests with well-developed undergrowth (Figure 13). Close to nothing is known about movements and home range in summer. Autumn migration to hibernation sites is usually conspicuous and synchronized, triggered by rains or mild cloudy conditions.

Hibernation in North Sweden is aquatic. It may take place in breeding wetlands if not prone to developing anoxic conditions in winter. However, in most cases *Rana temporaria* migrate to spend the winter in nearby well-oxygenated streams and rivers. There they seek shelter on the bottom in nearshore aquatic vegetation, but they will move to deeper water later in winter if the ice sheet expands downwards or if the water level recedes. Hibernation has also been observed in springs and natural wells in closed forest, as well as in brackish water in the Baltic (Elmberg *et al.* 1979). Terrestrial hibernation in the boreal is known from Norway (Frislid & Semb-Johansson 1981) and Finland (Pasanen & Sorjonen 1994) and may occur in North Sweden, although it has not been documented. Experimental work in Finland strongly indicates that the species cannot survive more than a few days of freezing temperatures at the most (Pasanen & Karhapää 1997), making it a much less likely terrestrial hibernator than *Rana arvalis*.

Abundance estimates and trends. Throughout the 1980's I studied two populations in Umeå, Västerbotten, at breeding sites encircled by built-up urban areas (Tvärån: 63°49'50.9"N, 20°13'38.4"E and Bölesholmarna: 63°49'31.4"N, 20°14'6.7"E). The summer foraging habitat surrounding these ponds comprises mid- to late successional riparian deciduous woodland (2.5 and 15 hectares, respectively; Figure 18). Counts of calling males at both sites and drift fence catch data from the Tvärån site permitted accurate estimates of population size (Elmberg 1990). Accordingly, the density of adult frogs in these summer habitats averaged 65–75/hectare (i.e., 6500–7500/km²). In the 1990's the isolated and far offshore island Stora Fjäderägg in Västerbotten (63°48'N 21°00'E; area ca 170 hectares) was subject to a census of spawn clumps in all its wetlands (Stefan Andersson, personal communication). Supposing an even sex ratio and that each female laid one egg clump, the island's population was 1200 adults (both sexes), that is, 7/hectare (700/km²). The density of adults in summer habitat on Low-Alpine heath well above treeline (Kraipe, Lycksele lappmark; 65°50'4.0"N, 16°22'23.0"E; altitude 780 m; Figure 17) was estimated at 2–4/hectare (200–400/km²) in a population studied by me for several years in the late 1980's.

The abundance estimates from the two Umeå sites are remarkably similar and probably close to the maximum occurring in North Sweden. Stora Fjäderägg and Kraipe, on the other hand, both represent suboptimal habitats. I propose that an abundance of 600 adults/km² is a realistic average value for North Sweden, from the Southern Boreal up to and including the Subalpine zone.

There are no indications of changes in abundance during the last 50 years.



FIGURE 5. Distribution of *Rana temporaria* in North Sweden. Although the entire Scandic Mountain range is colored, the species is absent from the High-Alpine zone in the Alpine region (see Figure 1 for outline of the latter). In other words, the species is missing from areas higher than 1400 m in Jämtland, decreasing to 1000 m in Torne lappmark. Colored parts of the Baltic are areas with widespread occurrence on offshore islands.

Moor Frog *Rana arvalis* Nilsson 1842

Distribution (Figure 6). Included records from *Artportalen* (N=650): as confusion with *Rana temporaria* is possible, reports from the Alpine region, the Northern Boreal region and all offshore sites were included only if substantiated by photos, concern calling males, or made by known experienced observers. Reports from the Southern and Middle Boreal were all included.

Widespread and common in the Southern and Middle Boreal. For unknown reasons more abundant in landscapes with flatter topography (Sterner 2005; Elmberg 2008), a pattern also noted in Finland (Terhivuo 1981). Widespread but less common in the Northern Boreal, scarce in its higher parts. The northernmost Swedish record is at Kulijärvi, Torne lappmark (67° 50' N, 21° 40' E; Elmberg 1984). Previous records from the Alpine region (e.g., Elmberg 1995) are now considered as unconfirmed and not valid.

The highest known records are very close to the border between the Northern Boreal and the Alpine regions: 580–600 m altitude at Danasjö-Abborrberg (Lycksele lappmark; Anders Forsgren personal communication) and 510 m at Årjep Kuossåive (Lule lappmark; Elmberg 1995; shown as an isolated occurrence in Figure 6).

Offshore occurrence of this species in the Baltic is a puzzling topic. Before the period covered here, Curry-Lindahl (1956) collected specimens on Haparanda Sandskär (Norrbotten), an island situated a staggering 32 km from the mainland. It has not been found there since. There are several recent reports in the *Artportalen* reporting platform (see Methods) from the offshore Holmön archipelago (Västerbotten), but none is convincingly documented. To conclude, there are no recent records of this species on truly offshore islands anywhere along the Baltic coast of North Sweden. This suggests a much lower dispersal capacity over brackish water than in the two other anuran species.

There are no indications of changes in distribution over the last 50 years. It should be noted, though, that the true range and abundance in North Sweden was grossly underestimated until the 1970's (Gislén & Kauri 1959 *versus* Elmberg 1978; 1984; 1995; 2008). The near-Alpine record from Härjedalen presented here (Figure 6; photograph in *Artportalen*) is the first from the province.

Habitat and movements. Spring migration usually starts 5–10 days later than in *Rana temporaria* (Elmberg 2008). Adult male *Rana arvalis* migrate to breeding sites in a strongly synchronized fashion during a few nights, whereas adult females have a more protracted spring migration. Juveniles are rarely seen before the end of the breeding season.

Breeds in a wide variety of wetland habitats: open mires, grassy bogs, forest lakes, flooded riverine meadows, deciduous bottomland forest swamps, and shallow brackish bays of the Baltic (Elmberg *et al.* 1979; Elmberg 2008; Figures 11, 14). Anthropogenic breeding sites include eutrophic ponds in agricultural settings as well as flooded disused gravel pits and quarries. Breeding *Rana arvalis* have an affinity for more richly vegetated wetlands than do the other two anurans, although spawning *per se* generally occurs in somewhat deeper water than in *Rana temporaria* (Elmberg 2008; cf. Ruuth 2017). Females remain in the breeding wetlands only until they have deposited their eggs, whereas adult males stay as long as receptive females are around, or longer (Elmberg 2008).

Dispersal from breeding sites to nearby summer foraging habitats is gradual and not very conspicuous. Summer habitats are varied, yet more restricted to well-vegetated and damp conditions than in *Rana temporaria*. In effect, *Rana arvalis* are rarely encountered in coniferous forest in summer, but more often in lush deciduous forest with a rich understory (Figure 18). However, most spend the summer in natural meadow-like habitats along lakes, rivers, and seashore, or in open grassy or willow-dominated habitats in forest clearings (Figure 13). Although there are not any quantitative data from North Sweden to verify the claim, it appears that *Rana arvalis* spend the summer closer to breeding sites than do *Rana temporaria* and *Bufo bufo* (cf. Čeirâns *et al.* 2021). In some areas and habitats of the interior north, such as open mires, adults appear to be semi-aquatic, spending most of the summer on grassy shores of breeding wetlands (Elmberg 2008; Figure 14).

In North Sweden, movement in summer has only been studied anecdotally by individual mark-recapture, suggesting a high degree of site fidelity (Elmberg 2008; see Ruuth 2017 for a telemetry study in nearby Finland documenting habitat preferences and movement distances).

Autumn migration to hibernation sites is sometimes conspicuous and synchronized, triggered by rains or mild cloudy conditions, and generally occurs a week or two earlier than in *Rana temporaria*.

Hibernation in North Sweden is aquatic, taking place in slow-flowing streams and rivers close to breeding sites, but sometimes in the latter or in nearby lakes. There, *Rana arvalis* seek out and settle in protective dense near-shore

aquatic vegetation, thus often hibernating alongside *Rana temporaria* and *Bufo bufo*. Note, though, that this species is extraordinarily cold-hardy and that terrestrial hibernation has been documented in Finland and Russia (Ruuth 2017; Berman *et al.* 2020). This may occur in North Sweden, too, although it has not yet been documented.

A fuller treatment in English of the ecology and natural history of *Rana arvalis* in North Sweden is found in Elmberg (2008).

Abundance estimates and trends. Throughout the 1980's I studied a population in Umeå, Västerbotten, at a breeding site encircled by built-up urban areas (Tvärån: 63°49'50.9"N, 20°13'38.4"E). The summer foraging habitat surrounding this pond comprises mid- to late successional riparian deciduous woodland (2.5 hectares; Figure 18). Counts of calling males and drift fence catch data permitted accurate annual estimates of the breeding population. Accordingly, the density of adult frogs in the summer habitat was 35–60/hectare (3500–6000/km²), depending on year. These densities represent a habitat that is probably among the most benign for this species in North Sweden. A more likely average abundance for North Sweden in general is in the interval 400–700 adults/km², with the lower densities in the Northern Boreal and the hilly parts of the Southern Boreal. These landscape level abundance estimates are fairly similar to those for *Rana temporaria*, a notion supported by impressions from roadside surveys of calling anurans in the interior of North Sweden (Elmberg 1984).

There are no indications of large-scale changes in abundance over the last 50 years (Elmberg 2008).

Viviparous Lizard *Zootoca vivipara* (Jacquin 1787)

Distribution (Figure 7). Included records from *Artportalen* (N=775): all reports have been included, as there are not any confusion species.

Widespread and common in the Southern, Middle, and Northern Boreal. Widespread but scarce in the Subalpine zone. Locally occurring above treeline in the Low-Alpine zone in favorable microclimates.

As expected, the highest known occurrences in the Scandic Mountain range are gradually lower towards the north: 1000–1050 m altitude in Härjedalen (Sånfjället and Flatruet), 740 m in Pite lappmark (west of Vuoggatjålme), and 690 m in Lule lappmark (Vastenjaure).

There is just one record from a truly far offshore island (Stora Fjäderägg, Västerbotten; Figure 7; Elmberg 1995). Although common in seashore habitats on the mainland along the entire Baltic coast of North Sweden, there are surprisingly few records even from nearshore islands. An exception may be the archipelago in southern Norrbotten, where the species occurs on some outer islands (e.g., Stor-Räbben and Vargön, green offshore area in Figure 7; Stefan Andersson, personal communication). For North Sweden as a whole, this indicates a limited dispersal capacity over brackish water.

There are no indications of changes in distribution over the last 50 years.

Habitat and movements. Found in almost any habitat offering a combination of basking sites and protective low vegetation. Favored natural habitats are forest edges and clearings, stony slopes, rock outcrops, sandy areas, and shores of lakes, rivers and the sea (Figures 12, 14). It often occurs among *Juniperus communis*, *Calluna vulgaris*, *Empetrum nigrum* and other plants typical of dry sun-exposed conditions. Closed forest, tall grass, and wet habitats are avoided. Anthropogenic habitats are widely used, for example clearings under powerlines, clear-cuts, edges of fields and meadows, stone walls, cairns, and roadsides (Figures 13, 19).

There have not been any dedicated studies of this species in North Sweden. As far as known, it spends the entire annual activity period in the habitats mentioned above. Daily and annual movements are not known but appear very limited. Subterranean hibernation sites are found in or close to the summer habitat, usually in south-facing situations.

Abundance estimates and trends. There are not any published abundance data, but estimates based on extensive field work in the Umeå area (Västerbotten) 1975–1994 run in the neighborhood of >500 adults/km² in representative landscapes near the coast (Elmberg, unpublished).

There are no indications of changes in abundance over the last 50 years.

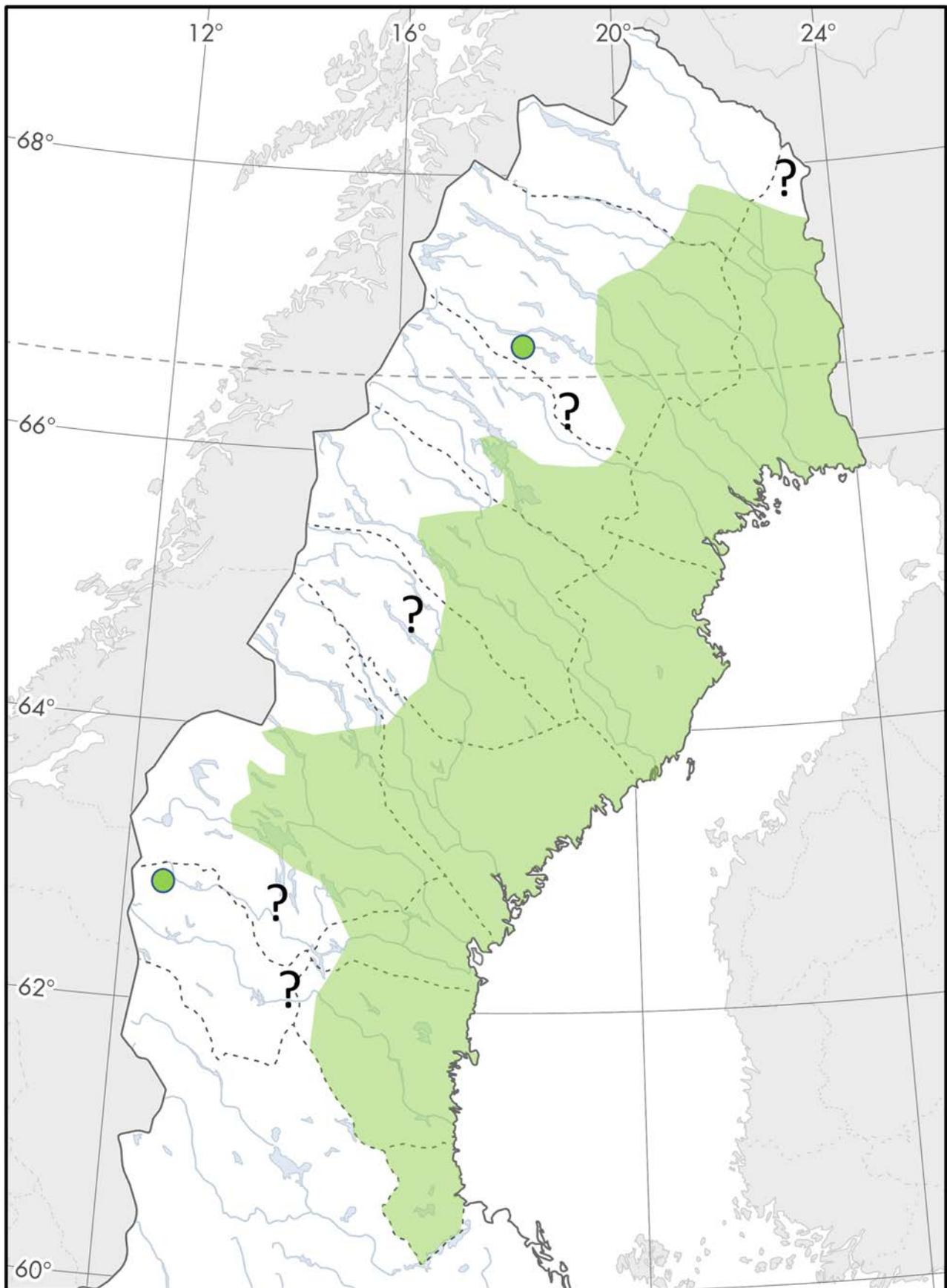


FIGURE 6. Distribution of *Rana arvalis* in North Sweden. Possibly disjunct records in Härjedalen and Lule lappmark are denoted by a filled circle. Question marks indicate areas where the shown range limit to the west and the north may be too conservative. There is not any documented recent occurrence on offshore islands in the Baltic.



FIGURE 7. Distribution of *Zootoca vivipara* in North Sweden. Although most of the Scandic Mountain range is colored, the species is absent from high-altitude areas in the Alpine region (see Figure 1 for outline of the latter). The upper limit of occurrence runs from 1100 m in Härjedalen, decreasing towards the north to 700–800 m in Lule lappmark. The only truly far offshore occurrence in the Baltic is shown by a triangle. A question mark denotes unknown status in parts of the vast Baltic archipelago in Norrbotten.

Slow Worm *Anguis fragilis* Linnaeus 1758

Distribution (Figure 8). Included records from *Artportalen* (N=360): as there are not any confusion species all reports have been included.

Common and widespread in the Southern Boreal and the coastal southern part of the Middle Boreal. From Medelpad and northwards all records have been made within 60 km of the Baltic coast.

The vast majority of records is from coastal areas or low altitudes in river valleys. Nevertheless, there are several records from above 300 m altitude in Hälsingland and Ångermanland, and a photo-documented occurrence at 425 m in Medelpad (15 km SW of Stöde).

Although most common near the coast, the total lack of records from offshore islands in North Sweden indicates poor dispersal capacity over brackish water.

There are no indications of changes in distribution during the last 50 years. Note, though, that the northernmost occurrence presented in the map (Figure 8; lower Byske River valley and the adjacent Tåme area to the north (Västerbotten)) became publicly known as late as 1989, despite the species having been known locally since at least the 1920's (Södermark 1989). This occurrence has long been regarded as a disjunct population (Elmberg 1995) and perhaps the result of anthropogenic spread, but recent records around Skellefteå have gradually closed the previously supposed 70+ km distribution gap.

Habitat and movements. In North Sweden this is the only reptile regularly encountered in closed forest, particularly in mesic stands with scattered deciduous trees and protective undergrowth. However, the most widely used habitats are fairly open, yet with denser undergrowth than those preferred by *Vipera berus* and *Zootoca vivipara*: forest edges, natural grasslands, shores, and rock outcrops. Most sightings of *Anguis fragilis* are made in anthropogenic habitats such as clear-cuts, fields, meadows, roadsides, and near recreational buildings (Figures 13, 19).

Although it is the only reptile in North Sweden frequently seen active in cloudy weather, its general habits are seclusive. Shelter is typically found under flat stones, haystacks, compost piles, sheet metal, woodpiles, and tarps, in other words often under man-made objects. This habit may facilitate inadvertent anthropogenic spread.

Daily and annual movements have not been studied, including any seasonal variation in habitat affinity.

Subterranean hibernation sites are most likely found in or very close to the summer habitat, but nothing is known about hibernation habits in North Sweden.

Abundance estimates and trends. There are not any published abundance data, but estimates based on extensive field work in the Umeå area (Västerbotten) 1975–1994 run in the neighborhood of >200 adults/km² in landscapes with mixed habitat near the coast (Elmberg, unpublished, Stefan Andersson, personal communication). There are no indications of changes in abundance over the last 50 years.

Grass Snake *Natrix natrix* (Linnaeus 1758)

Distribution (Figure 9). Included records from *Artportalen* (N=200): all reports from Gästrikland, Hälsingland, and coastal Medelpad (where widespread). Reports from other areas have been included only if documentation was available. This species and black morph *Vipera berus* are widely confused, even among naturalists.

Occurs throughout the Southern Boreal. Widespread and fairly common in Gästrikland and coastal Hälsingland, local and scarce in interior Hälsingland and coastal Medelpad. There is a disjunct well-documented record at 480 m altitude in central Härjedalen, in the Northern Boreal region (Figure 9). This is by far the highest known record, whereas the 2nd to 4th highest in North Sweden were all made at 180 m or lower. For the former extraordinary record there is no obvious suspicion of anthropogenic spread. However, well-documented records north of the present range (filled black circles in the map) can all be suspected to have anthropogenic origin, and none represents permanent presence or a reproducing population.

Although the species is an excellent swimmer there are just two records on offshore islands off the Baltic coast of North Sweden (Limön and Eggegrund, both in Gästrikland).

For the period 1900–1950, Gislén & Kauri (1959) listed many records in the Middle and Northern Boreal, far north and west of the known present range. Several were well documented, but it is not known whether those occurrences were relicts from a previously wider natural distribution, or the result of anthropogenic activities such as long-distance transport of hay and manure (Elmberg 1995). As late as the late 1960's there were confirmed records

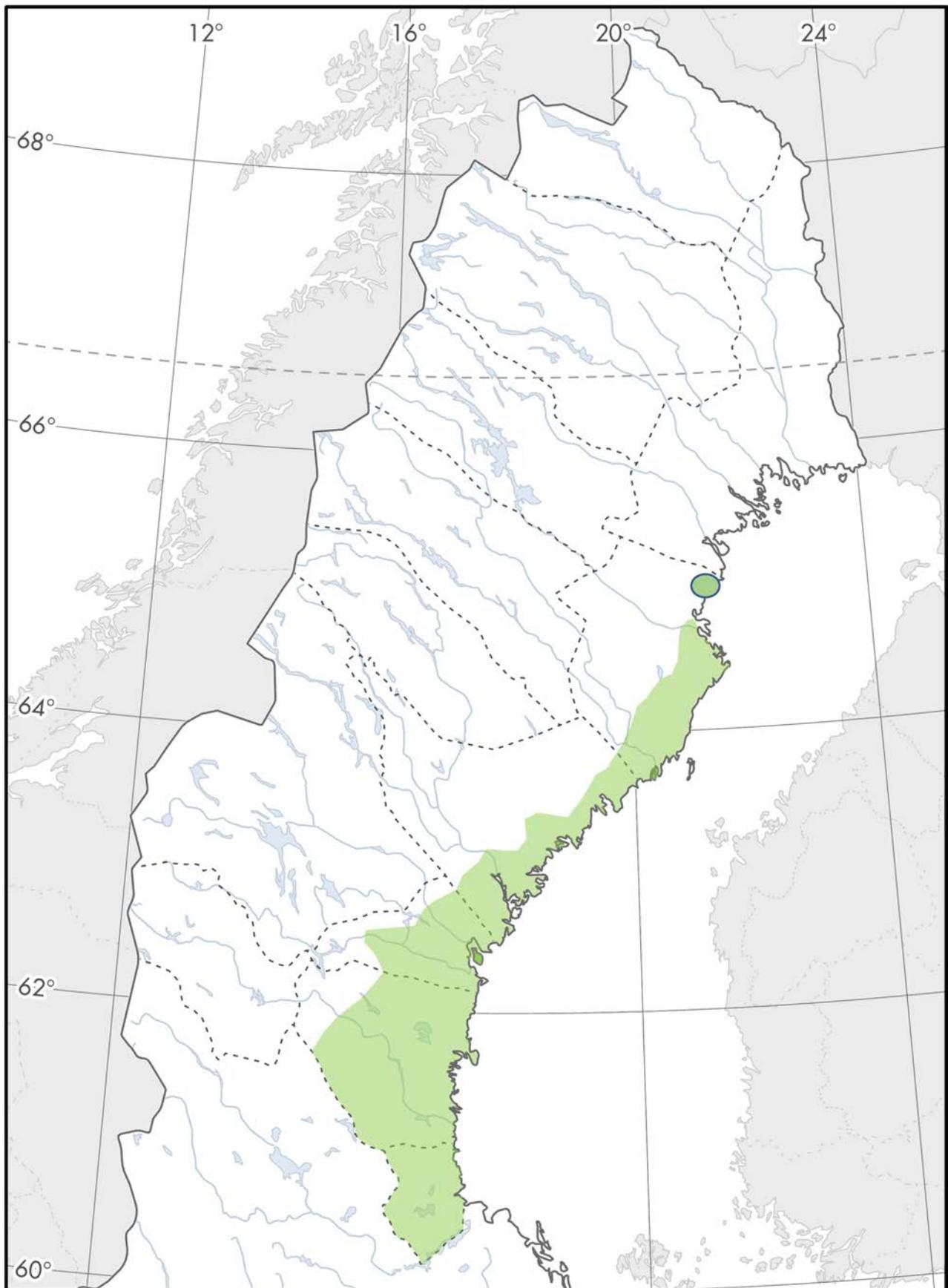


FIGURE 8. Distribution of *Anguis fragilis* in North Sweden. The oval in northernmost Västerbotten represents many records over a long time period, a population that is possibly disjunct. Note the total lack of records from offshore islands in the Baltic.

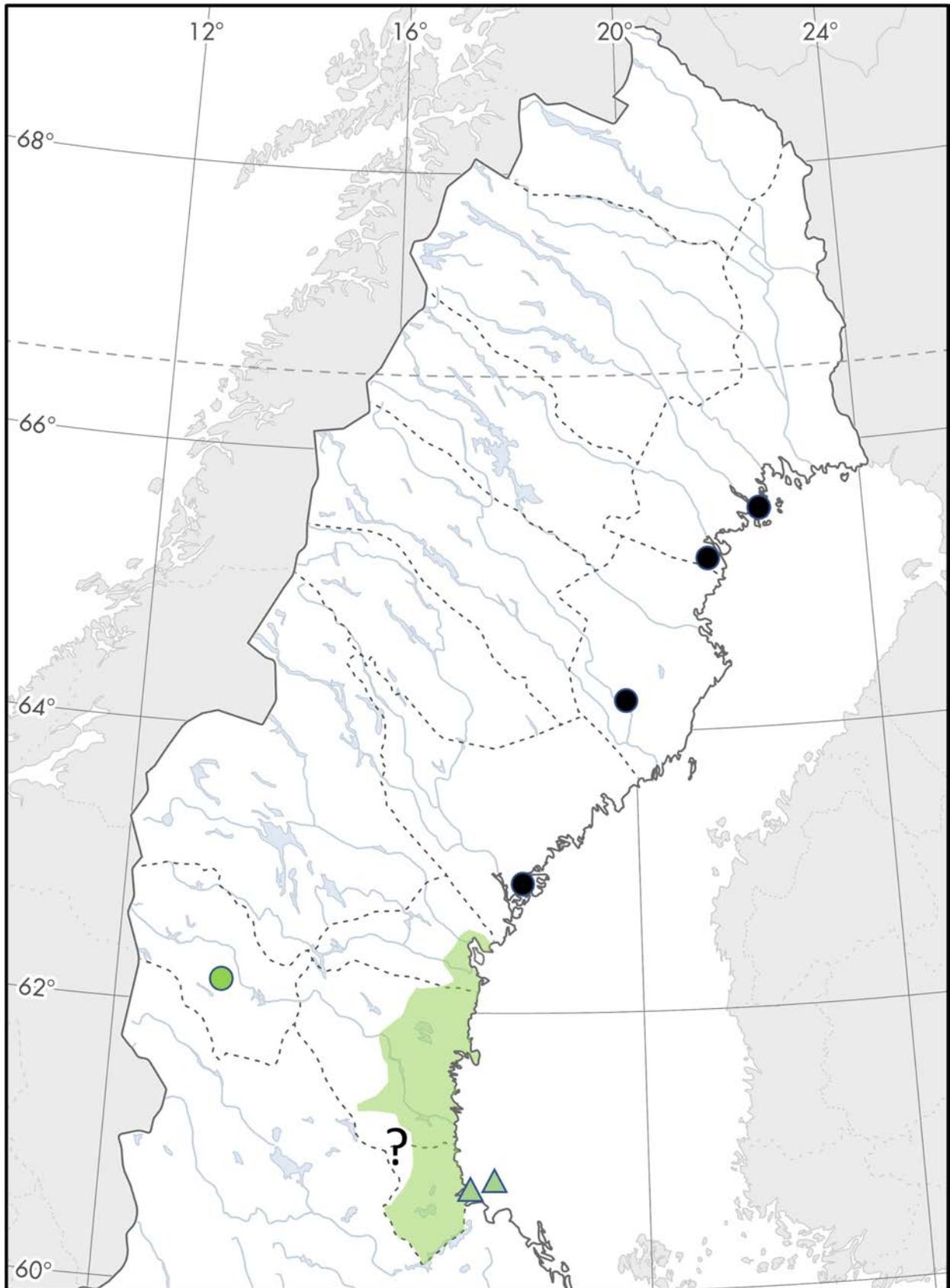


FIGURE 9. Distribution of *Natrix natrix* in North Sweden. The green circle denotes a disjunct record in Härjedalen, for which there is no suspicion of anthropogenic origin. Triangles show occurrence on far offshore islands in the Baltic. Filled black circles denote well-documented records where anthropogenic origin can be suspected (cf. Elmberg 1995). None of the latter represent permanent reproducing populations. A question mark shows area where presence is likely but has not been documented.

in several places around Umeå (Västerbotten, Middle Boreal; Stefan Ericsson personal communication), an area where the species has not been documented since. During the last 50 years, though, there have not been any indications of changes in distribution.

Habitat and movements. Found in open places providing shelter, such as tall field layer vegetation, cairns, stone walls, ditches, and heaps of plant debris. Typical habitats are shores of ponds and lakes, but also edges of fields and pastures. It is not known if habitat use varies over the annual activity period, but adult females must find suitable oviposition sites in early summer. This likely forces them to move considerable distances, probably through less typical habitats. All known oviposition sites in North Sweden were in composts, manure heaps or livestock fodder stacks (Löwenborg 2009; Mattias Hagman & Simon Kärverno, personal communication).

Although movements have not been studied in North Sweden, *Natrix natrix* are frequently seen crossing roads before and after oviposition (adult females) and after hatching in late summer (juveniles). This mobility sadly leads to many being killed by cars.

Nothing is known about hibernation habits in North Sweden, but communal hibernation at suitable south-facing sites is likely, as farther south in Sweden.

Abundance estimates and trends. There are not any data about abundance in North Sweden, nor any indications of changes in abundance over the last 50 years.

Adder *Vipera berus* (Linnaeus 1758)

Distribution (Figure 10). Included records from *Artportalen* (N=1250): all reports have been included. Any confusion between melanistic *Vipera berus* and *Natrix natrix* would not affect the distribution pattern.

Common and widespread in the Southern and Middle Boreal. Widespread and locally common in the Northern Boreal, where often found in areas of varied topography with south-facing slopes that offer early snowmelt and dependable hibernacula (Andersson 2003; Figure 20). Scattered observations have been made in the Subalpine and Low-Alpine zones (Curry-Lindahl 1975; Frislid & Semb-Johansson 1981; Elmberg 1995).

The highest reported occurrences show a slightly decreasing altitude from south to north: 940 m in Härjedalen (Flatruet), 900 m in Jämtland (Oviksfjällen), 720 m in Lycksele lappmark (Kraipe), but 820 m in Lule lappmark (Aktse). Most of these concern south-facing sites in the upper Subalpine zone, but also above treeline in the Low-Alpine zone. In the upper reaches of the river Lilla Luleälv (Lule lappmark) there are many records in the Aktse and Tarradalen areas (e.g., Cederberg 1974), suggesting widespread occurrence in the Subalpine zone there.

Widespread and locally abundant on many offshore islands along much of the Baltic coast of North Sweden (Figure 10), as is the case across the sea in Finland (Terhivuo 1981). An illustrative example is the Holmön archipelago in Västerbotten, where this species is abundant on islands >10 km from the mainland. This implies high dispersal capacity over brackish water.

There are no indications of large-scale changes in distribution over the last 50 years.

Habitat and movements. Males typically emerge from hibernation two weeks before females. Mating occurs near the hibernaculum, after which snakes disperse to summer habitats. The latter are largely the same as those of *Zootoca vivipara*: forest edges, forest clearings, stony slopes, rock outcrops, shrubbery, and shores of lakes, rivers, and the sea (Figure 12). In the vast interior of North Sweden summer habitats also include margins of bogs and mires (Figure 14). Areas providing a combination of basking sites and hiding places are favored. Anthropogenic habitats are widely used, too, for example clearings under powerlines, clear-cuts, edges of fields and meadows, and stone walls (Figures 13, 19). Very rarely found in closed forest, but sometimes in mature pine forest with natural gaps and clearings. It also occurs regularly in dense *Juniperus communis* thickets and in tall grass, where prey animals are likely to be found.

There are not any telemetry data available from North Sweden, but judging from field observations *Vipera berus* appears to be more mobile in summer than are *Zootoca vivipara* and *Anguis fragilis*. However, Andersson (2003) reported from the Northern Boreal that pregnant females may remain close to the hibernaculum throughout summer. The distance from summer habitats to hibernation sites can be up to 2 km (Andersson 2003), a journey during which *Vipera berus* can be found in other habitats.

Hibernation usually occurs in open south-facing locations with abundant crevices and underground access. Typical sites are talus slopes, stony moraine ridges (cf. Andersson 2003) and screes in the forest landscape (Figure 20),

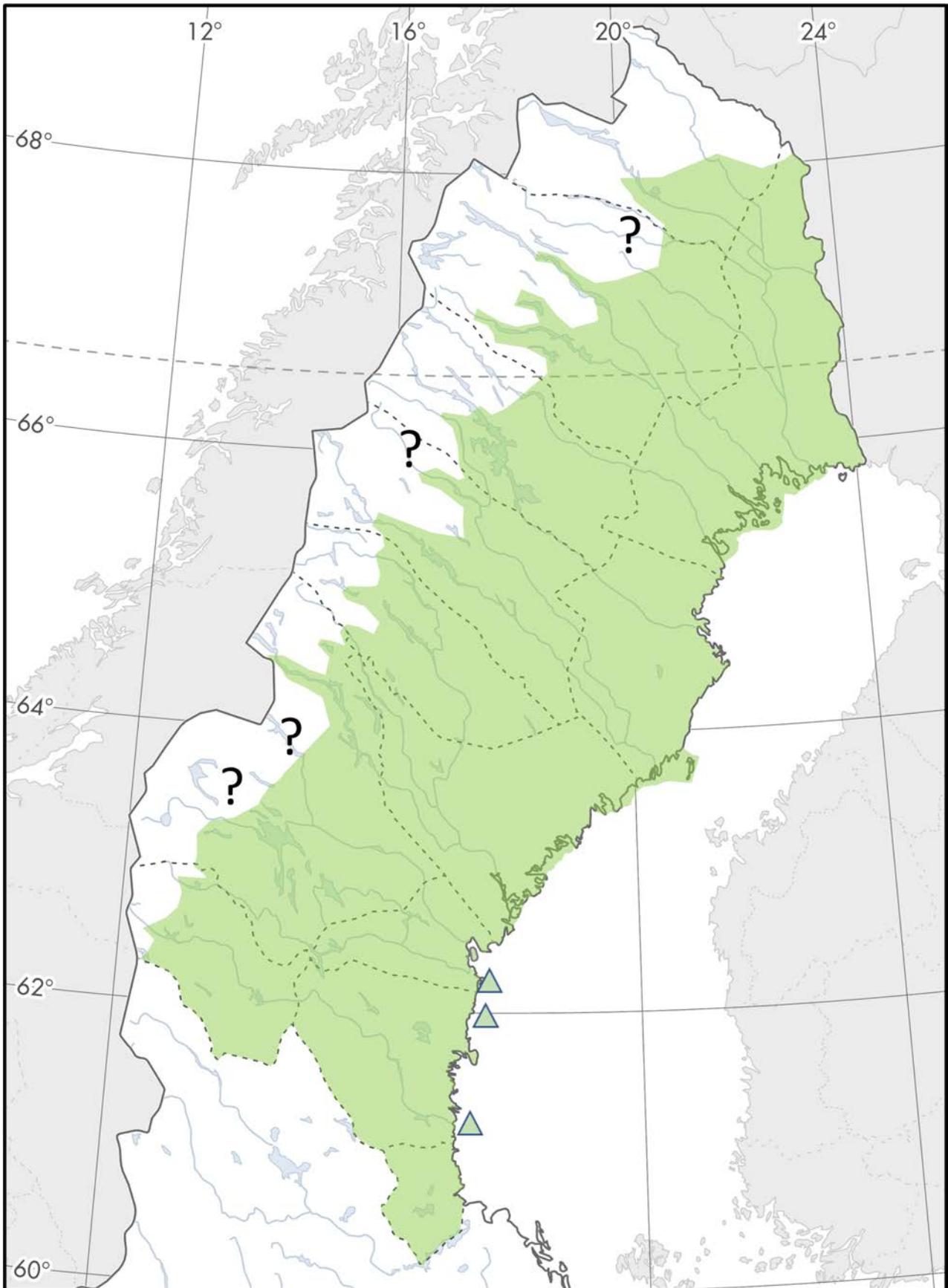


FIGURE 10. Distribution of *Vipera berus* in North Sweden. Colored parts of the Baltic in Ångermanland, Västerbotten, and Norrbotten represent areas with widespread occurrence on offshore islands. Triangles at sea in Medelpad and Hälsingland represent more singular offshore occurrences. Question marks denote areas where the western range limit is poorly known.

but also cairns if big and deep enough. Good hibernation sites are always well-drained and can attract individuals from a large surrounding area. There are reports from North Sweden that a single hibernaculum can host hundreds of individuals (Frislid & Semb-Johansson 1981).

Abundance estimates and trends. There are not any published abundance data, but estimates based on extensive field work in the Umeå area (Västerbotten) 1975–1994 run in the neighborhood of 50–100 adults/km² (Elmberg, unpublished). A mark-recapture study on the far offshore island Stora Fjäderägg (Västerbotten; 63°48'N, 21°00'E; area ca 170 hectares) suggests an average abundance of ca. 0.6 adults/hectare (60/km²) (Stefan Andersson, unpublished). However, studies by Stefan Andersson on the mainland suggest that abundance estimates for larger areas are particularly difficult to make in this species; adults occur within a certain radius of hibernacula, but between the latter there may be large areas of good summer habitat more or less devoid of adders.

There are not any true monitoring data for any period of the last 50 years, but recurrent visits to known sites of occurrence in southern Västerbotten indicate a steady and significant drop in abundance from the late 1970's to the present day (Elmberg, unpublished).

Anthropogenic changes in North Sweden: a herpetological perspective

Although human settlement in North Sweden dates back more than 9000 years, anthropogenic effects on amphibians and reptiles were negligible until late medieval times, and even then insignificant except very locally. The first land use changes to affect amphibians and reptiles more profoundly were deforestation and draining of wetlands to promote agriculture, processes that accelerated in the 1700s and 1800s. However, these were long mainly restricted to the more arable parts of the coastal lowlands and the lake Storsjön region in Jämtland, but in neither area likely affecting abundance or population connectivity of the herpetofauna in a landscape context.



FIGURE 11. Mesotrophic lakes with extensive beds of grasses and sedges provide breeding habitat for *Rana temporaria*, *R. arvalis*, and *Bufo bufo*. If fishless, also *Lissotriton vulgaris* is likely to occur in lakes of this type. Spring aspect from Öster-Skivsjön, Västerbotten, Middle Boreal region. Photo: Johan Elmberg.

TABLE 1. Occurrence of amphibians and reptiles by faunistic province (see Figure 1) in North Sweden 1970–2022. Occurrence by biotic regions and alpine life zones is described in the species accounts.

Faunistic province	<i>Lissotriton vulgare</i>	<i>Triturus cristatus</i>	<i>Bufo bufo</i>	<i>Rana temporaria</i>	<i>Rana arvalis</i>	<i>Zootoca vivipara</i>	<i>Anguis fragilis</i>	Matrix	<i>Vipera berus</i>
Torne lappmark	Not recorded	Not recorded	Not recorded	Widespread, common	Widespread in southeast	Widespread, common	Not recorded	Not recorded	Widespread but local
Lule lappmark	Not recorded	Not recorded	Widespread in southeast	Widespread, common	Widespread, common	Widespread, common	Not recorded	Not recorded	Widespread, common
Pite lappmark	Not recorded	Not recorded	Widespread, common	Widespread, common	Widespread, common	Widespread, common	Not recorded	Not recorded	Widespread, common
Lycksele lappmark	Four known localities	Not recorded	Widespread, common	Widespread, common	Widespread, common	Widespread, common	Not recorded	Not recorded	Widespread, common
Åsele lappmark	Not recorded	Not recorded	Widespread, common	Widespread, common	Widespread, common	Widespread, common	Not recorded	Not recorded	Widespread, common
Jämtland	Widespread, but local	Widespread, but local and rare	Widespread, common	Widespread, common	Widespread, common	Widespread, common	Not recorded	Not recorded	Widespread, common
Härjedalen	Not recorded	Not recorded	Widespread in far east	Widespread, common	One record	Widespread, common	Not recorded	One record	Widespread, common
Norrbotnen	Two known localities	Not recorded	Widespread, common	Widespread, common	Widespread, common	Widespread, common	Not recorded	Documented records, but no known recent reproduction	Widespread, common
Västerbotten	Widespread, but local	Not recorded	Widespread, common	Widespread, common	Widespread, common	Widespread, common	Widespread, common	Documented records, but no known recent reproduction	Widespread, common
Ångermanland	Widespread	Widespread, but local	Widespread, common	Widespread, common	Widespread, common	Widespread, common	Widespread, common	Documented records, but no known recent reproduction	Widespread, common
Medelpad	Widespread	Widespread	Widespread, common	Widespread, common	Widespread, common	Widespread, common	Widespread, common	Restricted, locally common	Widespread, common
Hälsingland	Widespread	Widespread	Widespread, common	Widespread, common	Widespread, common	Widespread, common	Widespread, common	Widespread, common	Widespread, common
Gästrikland	Widespread	Widespread	Widespread, common	Widespread, common	Widespread, common	Widespread, common	Widespread, common	Widespread, common	Widespread, common



FIGURE 12. Ongoing post-glacial land uplift creates open habitats along the Baltic coast of North Sweden. Rock pools (foreground) serve as breeding sites for *Rana temporaria* and *Bufo bufo*, occasionally also for *Lissotriton vulgaris*. Brushy areas along the forest edge (background) are typical summer habitat for *Zootoca vivipara* and *Vipera berus*. Tjäruskär, Ångermanland, Middle Boreal region. Photo: Johan Elmberg.

It is fair to assume that the anthropogenic footprint became significant beyond the local only in the late 1800s, when forestry and agriculture were expansive enough to become prevalent in the Southern Boreal and the Middle Boreal biotic regions. Selective cutting of old growth forest created clearings and ecotones that probably benefitted reptiles. On the other hand, beginning in the late 1800s state-subsidized large-scale draining operations eliminated many wetlands suitable for amphibians in many parts of North Sweden. There are, however, no historical quantitative data about amphibian and reptile population declines to verify the impact of these operations.

New forestry practices adopted after World War II include the use of large clear-cuts and replacing natural forests with plantation type stands. This has brought about a massive ecological change, as only a few percent of the forest land is set aside as reserves and permitted to develop naturally. However, reptiles are rarely found in the forest interior in North Sweden, including in natural old growth, but rather prefer open habitats and forest edges (see species accounts above, but cf. Čeirāns 2002; 2004). Hence, it is likely that clear-cuts and early successional stages post-felling, typical of modern forestry, rather have benefitted reptiles, as has been implied in an English study (Jofré *et al.* 2016). On the other hand, *Lissotriton vulgaris* and *Triturus cristatus* are supposedly negatively affected by forestry; many of the descriptions of their breeding wetlands in the Southern Boreal feature an abundance of down logs and coarse woody debris in mature forest around them (Sternér 2005; Olofsson *et al.* 2008, cf. Pabijan *et al.* 2023). Such habitats may provide crucial terrestrial habitat and hibernation sites, but have unfortunately been clear-cut at many breeding wetlands recently (Persbo *et al.* 2006; Olofsson *et al.* 2008)



FIGURE 13. Recently abandoned hayfields are prime summer habitat for *Rana temporaria*, *R. arvalis*, *Bufo bufo*, *Anguis fragilis*, and *Vipera berus*. The forest edge in the background is typical habitat also for *Zootoca vivipara*. Baggböle, Västerbotten, Middle Boreal region. Photo: Johan Elmberg.



FIGURE 14. Vast areas of North Sweden's interior are covered by level open bogs with permanent water. *Rana temporaria*, *R. arvalis*, and *Bufo bufo* breed in the pool depressions (foreground) and come ashore to forage in grassy areas in summer. More elevated and drier string parts of the bogs offer protective vegetation and summer habitat for *Zootoca vivipara* and *Vipera berus*. Photo: Jonas Grahn.



FIGURE 15. Summer habitat for *Rana temporaria* in the transition between the Mid- and High-Alpine life zones. Here the annual activity period lasts three months or less, during which adults adopt a semi-aquatic lifestyle, spending much time in small creeks and seepage areas. Stekenjokk, Jämtland, 1070 m altitude. Photo: Johan Elmberg.

Another important feature of modern forestry is draining to make stands drier to increase timber production. Tens of thousands of small forest wetlands in North Sweden have been lost in this way over the last 100 years. This habitat loss and the resulting fragmentation cannot have been positive for amphibians, but to what extent population trajectories have been affected large scale is not known (Elmberg 1993; Remm *et al.* 2018).

Introduction of salmonid fish (Salmonidae) and *Esox lucius* (Pike) to lakes to promote fishing has been a common and geographically widespread practice in North Sweden (Henriksson *et al.* 2016). At least newts and frogs – breeding adults as well as larvae – are vulnerable to predation by these fish. Fish stocking practices have led to local extinctions of amphibians in North Sweden (see species accounts above for *Lissotriton vulgaris* and *Triturus cristatus*), but there are no data to quantify this impact beyond the few known cases.

Deposition of acidifying compounds by rain was a significant environmental issue throughout Sweden in the 1980's and 1990's. In these decades, studies in northern Europe showed that anuran egg development is sensitive to low pH levels (e.g., Räsänen *et al.* 2003). As a result, acidification was long seen as a serious threat to amphibians in North Sweden, not least because most wetlands below the Alpine region are naturally acidic and have low alkalinity. In more recent decades, the amounts of acidifying compounds in precipitation over North Sweden have decreased (Laudon *et al.* 2021). Little is known about how naturally low pH levels and previous acidification have affected amphibian populations in North Sweden.

Interestingly, but perhaps not so surprisingly, the long run of mild years 1990–2022 has not resulted in any apparent northward range extension in amphibians and reptiles in North Sweden. The species in question are slow dispersers and will likely require a longer period of climate amelioration to respond to such change. However, temporal shifts towards earlier spawning in anurans and earlier appearance from hibernation in reptiles are already evident, amounting to a week or more from the 1980's to the present day (Elmberg, unpublished; Stefan Andersson, personal communication).

It is striking that habitats characterized by early and moderate anthropogenic influences, are important to reptiles in the present day. Indeed, they are often most easily encountered in such environments. Ecotones between agriculture (fields and pastures) and forest are prime habitats for all four reptile species in North Sweden. Parts of the habitat patchwork generated by modern forestry, that is, ecotones between forest edge and open clear-cuts, are utilized by *Vipera berus* and *Zootoca vivipara*. In addition, some truly man-made habitat features seem crucial for *Natrix natrix* (compost piles and manure heaps for egg-laying) and *Anguis fragilis* (hiding places close to settlements and farms).



FIGURE 16. *Rana temporaria* is the hardest amphibian in North Sweden, ranging up to the transition between the Mid- and High-Alpine life zones. Individuals in these uppermost populations often give a toad-like impression due to their dark color and short hindlimbs. Stekenjokk, Jämtland, 1070 m altitude. Photo: Johan Elmberg.

These observations of the present day beg the question of what were the habitat affinities of the herpetofauna of North Sweden for thousands of years, before man affected the landscape. Amphibians probably found ample habitats for breeding, summer foraging, and hibernation, like those used today, although with somewhat less compromised connectivity. Semi-open habitats suitable for reptiles were likely found in and around talus slopes, along rivers, lakes, and seashores, as well as in open wetlands with a varied micro-topography (e.g., mires with pool-tussock mosaic). More speculatively, natural forest fire dynamics may have created openings and patchy habitat mosaics suitable for reptiles in the boreal landscape. At any rate, many of the habitats utilized by amphibians and reptiles in pristine

times were ecotones and other linear landscape elements. The boreal forest interior must always have been little utilized, and connectivity between suitable habitat patches must have been a challenge also before anthropogenic change came about.



FIGURE 17. *Rana temporaria* is the only amphibian breeding in alpine heath habitats well above tree line in the Scandic Mountains of North Sweden. Among the variety of wetland types available, chorusing and spawning invariably take place in shallow ponds with moderate to sparse vegetation. Despite high altitude and latitude, a short annual activity period, and a cool overall climate, breeding ponds enjoy constant daylight, high insolation and thus warm up rapidly. Kraipe, Lycksele lappmark, 820 m altitude, Low-Alpine zone. Photo: Johan Elmberg.

Recent concerns for the herpetofauna are road mortality, invasive species, and novel diseases. Roads cover minute areas in North Sweden, but unfortunately often pass through habitats suitable for amphibians and reptiles. Massive road mortality of all anuran species can be observed during spring migration to breeding wetlands. Among the reptiles, *Vipera berus* and *Anguis fragilis* are the most commonly observed roadkills, mainly in warm summer weather. There is no information about the impact of road mortality in North Sweden, but likely it is quite local and not a major concern. No invasive species have been demonstrated to significantly affect amphibians and reptiles in North Sweden. However, *Neovison vison* Schreber (American Mink) is widespread and known to voraciously consume frogs in the boreal (Ahola *et al.* 2006). *Nyctereutes procyonoides* Gray (Raccoon Dog) – a known problem predator for amphibians – has not yet colonized Sweden large-scale, but it is widespread in nearby Finland. In a recent study Meurling *et al.* (2020) did not find the chytrid fungal disease *Batrachochytrium dendrobatidis* in *Rana arvalis* in North Sweden. However, the pathogen is widespread in central and southern Sweden, and there found to infect several amphibian species.

The official conservation status of amphibians and reptiles in North Sweden is presented in the national Swedish Red-list (www.artdatabanken.se/en/).



FIGURE 18. Summer habitat for *Rana temporaria* and *Rana arvalis* in boreal riparian deciduous woodland. The canopy is dominated by *Alnus incana*, *Prunus padus*, and *Sorbus aucuparia*, with scattered *Salix caprea* and *Betula pubescens*. The lush herbaceous field layer provides shelter and abundant invertebrate food in summer. Population density at this site has been estimated at up to 7500 and 6000 adults/km² of *Rana temporaria* and *R. arvalis*, respectively. Bölesholmarna, Umeå, Västerbotten, Middle Boreal region. Photo: Johan Elmberg.

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FIGURE 19. Clear-cuts offer summer habitat for *Zootoca vivipara*, *Anguis fragilis*, and *Vipera berus* for a decade or so until planted conifers grow tall enough to shade the ground. Robertsfors, Västerbotten, Middle Boreal region. Photo: Johan Elmberg.



FIGURE 20. Talus slopes and screens provide communal hibernation sites for *Vipera berus*, offering frost-free conditions also in case of early winter weather with little insulating snow cover. Such sites invariably face SW–SE and have early snowmelt that permits earlier spring emergence than in surrounding areas. Mating usually takes place here, after which vipers disperse to summer habitats visible in the background. This picture is from one of the northernmost known hibernation sites in Sweden at 68°N. Etnoluhtinvaara, Torne lappmark, Northern Boreal region. Photo: Stefan Andersson.

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