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# Habitat Analyses of the Amphibian Populations on the Baltic Island Gotland

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# Contents



**Cover photos:** Vestlands myrarna, a twig rush mire (agmyr) outside Burgsvik (southern Gotland). This mire is an important breeding site for the amphibian species occurring on Gotland. The inserted picture shows spawning moor frogs *(Rana arvalis)* in the mire (photographer the author).

## Summary

The dependence on two habitats, one terrestrial and one aquatic, makes amphibians in general more vulnerable to landscape changes than other organisms. The aim of this study was therefore to examine the influence of aquatic and terrestrial variables on the amphibian community on Gotland. Three species are present on the Baltic Island Gotland, *Rana arvalis*, *Bufo bufo* and *Triturus vulgaris*. To find out which variables that best explains presence or absence of each of the three amphibians, 314 potential breeding sites were analysed with 39 aquatic and 22 landscape variables, even the influences of land use changes were taken into account. *R. arvalis* showed a clear preference for sun exposed large and permanent waters with oligotrophic water plants. Surroundings of deciduous forest and wetter marshes were positively and surroundings of agriculture, cut forest and sea were negatively associated with occurrence of the frogs. *B. bufo* was associated with similar variables, but the associations were generally much weaker than for the frogs. *T. vulgaris* was positively associated with pools and negatively associated with fish and watering ponds. *B. bufo* and *R. arvalis* occurred in squares where the agricultural land-usage was low. A favourable local climate, higher water quality and permanence seems to be of general importance for the examined amphibian populations. However, this study suggests *B. bufo* and *T. vulgaris* to be generalists, and *R. arvalis* a specialist in breeding site selection. Even the landscape variables seemed to have little importance for the two generalists, in contrast to *R. arvalis* that was clearly negatively affected by the modern land use. *R. arvalis* and *B. bufo* were probably more widespread earlier in history. This project could give a contribution to the understanding of the amphibian declines and be useful in management of the Gotlandic amphibians, in particular for *R. arvalis* which is considered to be an evolutionary significant unit on Gotland.

## Introduction

The 19th-century landscape has been going through radical changes, foremost in the industrial world. Large quantities of wetlands and pastures have been drained and cultivated, and the land used for agriculture and silviculture has expanded as a result of this use. As a consequence the biodiversity has decreased drastically in the cultivated areas. In Sweden 70% of the threatened vascular plants (Mattiasson 1993, Götmark et al. 1998), 33 % of the threatened fungi and 30% of the threatened birds reside on cultivated land and are negatively influenced by modern land use (Götmark et al. 1998).

In Sweden amphibians are the vertebrate group that have the highest proportion threatened species (70%) in the cultivated areas (Ahlén and Tjernberg 1996). What makes amphibians more vulnerable to land use changes than other organisms is their dependence on two kinds of habitats: an aquatic for their reproduction and a terrestrial for the adult stage (Duellman and Trueb 1986, Dodd and Cade 1998, Alford and Richards 1999). As slow moving ground dwelling organisms their recolonisation abilities are limited (Blaustein et al. 1994). The risk of extinction of local populations is therefore very high if only fragments of their habitats remain (Levins 1969), which normally is the case in cultivated areas. During the last decades amphibian declines have been reported all over the world (Blaustein and Wake 1990, Alford and Richards 1999, Alford et al. 2001), and the lack of general information on which environmental factors that harm amphibians has been actualised. Studies of three newt species in France showed that the proportion of agricultural land around a pond had a strongly negative effect on the newt abundance (Joly et al. 2001). Furthermore, studies in the USA suggest that distribution and abundance of amphibians are negatively effected by silviculture (Demaynadier and Hunter 1998, Lowe and Bogler 2002).

The island of Gotland is situated in the southern part of the Baltic Sea and 70% of the Gotlandic wetlands have been dried during the last centuries (Martinsson 1997), mostly for purposes of cultivation. These changes make Gotland quite representative of the land use change in Europe. What gave a study on Gotland unique possibilities was the access to cadastre maps from the beginning of the 18th-century with detailed land use information. Thanks to the Swedish kings' need of tax revenue we now have a good picture of historical mire land (mainly dominated by *Caldium mariscus* which was important cattle food and roof material), meadow, pasture and - of course - agricultural land distribution (Martinsson 1997).

*The physical geography of Gotland*
The bedrock on Gotland mostly consist of tight reef limestone, flatted by the glaciations (Fredén 1998). This geomorphological structure results in plane wetlands that mostly get the water from precipitation, not from nutrient rich surface water as in other parts of Sweden. The wetlands on Gotland are therefore generally more nutrient-poor and limy compared to the mainland wetlands. One type of Gotlandic wetlands are called *vätar*. They are formed by hollows in the bedrock. During autumn and winter they are filled up with rainwater, but because of the tight bedrock they do not get drained. The only way that the water can disappear is by evaporation, and because of the dry Gotlandic springs and summers, the wetlands dry up annually. This is mostly a vegetation poor environment that supports different plant communities. One of them, *Blekvät* is unique for Gotland and is characterised by lime precipitation from *Chara* vegetation. The most common plant community on Gotland is twig rush mire (*agmyr*). These mires are dominated by twig rush *Caldium mariscus* in the middle where it is wetter and surrounded by *Carex* tussocks (mainly *C. lasiocarpa* and *C. elata*) at the margins, where it is drier. *C. mariscus* is dominating the nutrient-poor wetlands, but is getting replaced by *Phragmites australis* and *Scirpus lacustris* in more nutrient rich wetlands. *Typha latifolia* and *Potamogeton natans* are dominating the eutrophic wetlands in the agricultural areas. *P. natans* is also often found in older cattle ponds (for more information see Martinsson 1997).

## The amphibians of Gotland

At present only three of the fourteen Swedish amphibian species occur on Gotland, *Rana arvalis* (Moor frog) *Bufo bufo* (Common toad) and *Triturus vulgaris* (Smooth newt). *Bufo viridis* (Green toad) was reported from a few localities (Gislén 1942), but went extinct from the island during the 1950:ies (Andrén and Nilson 2000).

*Rana arvalis* has a wide distribution in Eurasia from Scandinavia in the north, central and Eastern Europe in the south to eastern Siberia in the east (Arnold and Burton 1977, Engelmann et al. 1986, Fog et al. 1997, Gasc et al. 1997, Kuzmin 1999). The morphological and genetical variation within the distribution area is large and several subspecies have been described (Stugren 1966, Fog et al. 1997, Babik and Rafinski 2000, Rafinski and Babik 2000). In Sweden it is distributed all over the country except in the mountains of the north (Gislén and Kauri 1959, Elmberg 1978, Cedhagen and Nilson 1991, Ahlén et al. 1992). It occurs in a number of different habitats, and in general, it seems to prefer lowlands such as riverbanks, large marshes and often nutrient-poor acidic moor lands (Arnold and Burton 1977, Engelmann et al. 1986, Podloucky 1987, Ahlén et al. 1992, Fog et al. 1997, Gasc et al. 1997, Kuzmin 1999). In Sweden it is the dominant amphibian species in acidic bogs on the south Swedish highlands (Cedhagen and Nilson 1991, Fog et al. 1997). The general impression of the habitat choice seems to differ in different parts of Sweden. Hansen (2001) did a study from the surroundings of Lindköping (south-eastern Sweden) and found that *R. arvalis* was positively associated with agricultural and grass land, and negatively associated with oak pastures. Small water bodies with submerged and surface crossing vegetation were favoured as reproduction sites, waters with closed canopy or fish were not. Also in Uppland (eastern Sweden) it is the dominating frog in the agricultural areas (Juha Merilä pers. comm.), in Värmland (mid west Sweden) it seems to be associated with pine forest and agricultural land avoiding spruce forest (Berglind 1991). In Scania (southern Sweden) it is dominating in the nutrient-poor forestall areas in the northern part of the county (Berglund 1976). The habitat choice in western Europe resembles that in Scania; *R. arvalis* seems to be associated with nutrient-poor moor land and forests (Fog 1993, Vos and Chardon 1998). In Western Europe *R. arvalis* has declined radically during the last decades mainly because of increasing habitat fragmentation (Clausnitzer 1987, Fog 1993, Vos and Chardon 1998), and therefore the species is listed in the Bern Convention for European species in danger (Corbett 1989).

*Bufo bufo* is also widespread over most of Europe and Asia, from the British Isles and the Iberian peninsula in the west through Russia to Japan in the east (Arnold and Burton 1977, Engelmann et al. 1986, Fog et al. 1997, Gasc et al. 1997, Kuzmin 1999). Some subspecies have been described (Engelmann et al. 1986, Kuzmin 1999). In Sweden it is distributed all over the country except in the northern inland, and it is also the only amphibian on the Baltic island of Gotska Sandön (Gislén and Kauri 1959, Cedhagen and Nilson 1991, Ahlén et al. 1992). *B. bufo* seems to be a generalist within most of its distribution range. In many areas it is the most common amphibian, and occupies a wide range of habitats such as arable fields, grasslands, forests and even urban areas (Arnold and Burton 1977, Engelmann et al. 1986, Barbadillo 1987, Galán and Fernández 1993, Fog et al. 1997, Gasc et al. 1997, Barbadillo et al. 1999, Kuzmin 1999, Ensabella et al. 2003). It is also known for spawning in waters rejected by other amphibians such as shallow rock pools, large lakes with a high density of predatory fish, streams, creeks and even directly in the Baltic sea. Recently there have been reports of declining *B. bufo* populations in the Southeast of England (Carrier and Beebee 2003).

*Triturus vulgaris* is also spread over most of the central and northern Europe, from Ireland and Great Britain in the west to Siberia in the east, and seven subspecies have been described (Arnold and Burton 1977, Engelmann et al. 1986, Griffiths 1995, Fog et al. 1997, Gasc et al. 1997, Kuzmin 1999). The distribution covers most of Sweden with the northern limit in the north of Norrland (Gislén and Kauri 1959, Dolmen 1983, Cedhagen and Nilson 1991, Ahlén et al. 1992, Griffiths 1995). *T. vulgaris* occupies a number of different habitats and is often the most common newt species within its European distribution (Griffiths and Mylotte 1987, Griffiths 1995, Kuzmin 1999). It is found in agricultural areas, forests, grasslands and urban areas. It can breed in rock pools (salinity tolerance to 4 ‰, Fog et al. 1997) creeks and garden ponds, and show a higher tolerance to predatory fish than its relative *T. cristatus* (Dolmen 1982). *T. vulgaris* is generally more connected to small waters and is less common in lakes (Beebee 1981, Fog 1993, Griffiths 1995).

*Biodiversity on Gotland versus mainland*

The low amphibian diversity in Gotland follows the prediction from island-mainland biogeographic theory. Diversity tends to decrease with increasing distance to the mainland and decreasing island area (MacArthur and Wilson 1967). Restricted gene flow and small population sizes lead to increased importance of random genetic drift. Furthermore, if the selection pressures differ between the island and mainland, genetic and morphological differentiation can occur (Grant 1998). In the long run new species can be produced as a consequence of the genetic isolation (Grant 1998). However the last glaciation ended in southern Scandinavia only 10 000 years ago, and genetic differentiation is inversely correlated to the generation time (amphibians have long generation times especially in northern latitudes). The speciation process of the Gotlandic amphibians are therefore not expected to have had enough time for a substantial genetic differentiation (Lindgren 2001). Moreover it is not clear how isolated the Gotlandic amphibians really are. Brackish water is not a problem for *B. bufo* (Seppä and Laurila 1999) and the brackish water in the southern Baltic Sea (7 ‰ salinity) is probably not a impermeable matrix to cross for adult *R. arvalis* (Lardner 2000). The distance to the closest amphibian populations on Öland is about 50-km. There are some studies indicating genetic differentiation between the Gotland and mainland *R. arvalis* populations (Nilson and Andrén 1981, Lardner 1995, Lindgren 2001, Laurila et al. 2002), and the Gotlandic population has lost genetic diversity by a founder effect or a bottleneck (Lindgren 2001). However, Lindgren (2001) did not find evidence for the Gotlandic population to be considered as a separate subspecies, but as perhaps as an evolutionary significant unit. No morphological studies have been done on the other two species but recent phylogeographic research on *T. vulgaris* found evidence for colonisation from the east (Eevi Karvonen pers. comm.). Several factors could cause different selection pressures on Gotland versus the mainland. For all Gotlandic amphibians there are fewer competing species. On the mainland *R. arvalis* coexist with *R. temporaria* and / or *R. dalmatina*. *B. bufo* partly coexists with *B. calamita* and /or *B. viridis* and *T. vulgaris* coexists with *T. cristatus*. Reduced interspecific competition is known to cause changes in habitat preferences in other organisms (Alatalo et al. 1986). The wetlands on Gotland are mostly limy and nutrient poor, which could have caused adaptations in the larval stage to nutrient poor water, and make the Gotlandic amphibian populations more vulnerable to eurtophication. The nitrate stress tolerance in larval of *R. temporaria* is known to be higher in populations situated in the more eutrophic part of Sweden (Johansson et al. 2001).

*The aim of this study*

The aim of this study was to examine which aquatic and terrestrial habitat variables that best explain the occurrence of each of the three amphibian species on Gotland. Furthermore I aimed to build up models (useful in conservation) of significant factors explaining occurrence with as high agreement with observed data as possible. I also wanted to examine the importance of the land use changes during the last centuries in explaining possible amphibian declines on Gotland.

The study was split in two main parts, one that describes the censused water bodies, mainly with field data, and one that describes the proportion of landscape types 500 and 1000 meter around the censused water respectively.

# Methods

## Study area, census method and distribution of the Gotlandic amphibians

The study was carried out on the Swedish island of Gotland (57° 30′N, 18° 20′E) in the Baltic Sea. A total area of 250 square kilometres, distributed in ten squares was censused. One square (25 $km^2$) corresponds to one sheet on the Swedish cadastre map (fastighetskartan) grid system (scale 1:10000). The local authorities chose eight of the maps on the basis of containing high proportion of wetlands. The other two were chosen because of high proportion of agricultural land. The aim was to get a representative distribution of Gotlandic landscape in the examined area. Three persons, Juha Merilä, the autor and Johan Nilsson

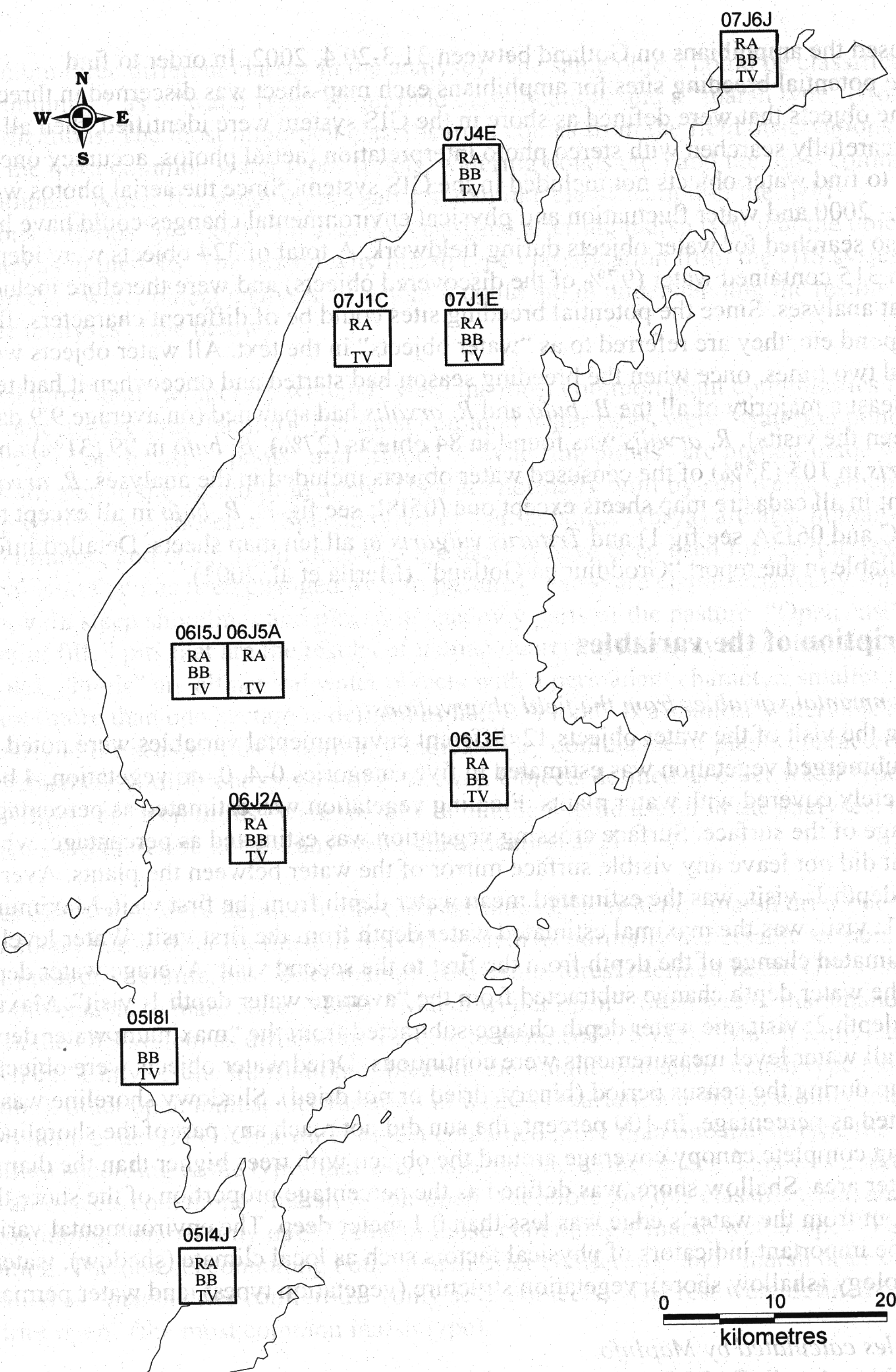


Fig 1. Censused cadastre map sheets (5 x 5 km) on the Baltic Island Gotland. The identification numbers are the codes in the Swedish national grid system, RA indicate presence of *R. arvalis*, BB indicate presence of *B. bufo* and TV indicate presence of *T. vulgaris* in the map sheets. Map sheet 06J5A and 07J1C were chosen because of high proportion of agricultural land and the other map sheets were chosen because of high proportion of wetlands.

censused the amphibians on Gotland between 31.3-20.4, 2002. In order to find all the potential breeding sites for amphibians each map-sheet was discerned in three steps. All the objects that were defined as shore in the GIS system were identified, then all maps were carefully searched with stereo photo interpretation (aerial photos, accuracy one $m^2$) in order to find water objects not included in the GIS system. Since the aerial photos were taken 1999 – 2000 and water fluctuation and physical environmental changes could have happened, we also searched for water objects during fieldwork. A total of 324 objects were identified, of which 315 contained water (97% of the discovered objects) and were therefore included in the habitat analyses. Since the potential breeding sites could be of different characters, flood, lake, pond etc. they are referred to as "water objects" in the text. All water objects were visited two times, once when the breeding season had started and once when it had terminated or at least a majority of all the *B. bufo* and *R. arvalis* had spawned (on average 9.9 days between the visits). *R. arvalis* was found in 84 objects (27%), *B. bufo* in 99 (31%) and *T. vulgaris* in 105 (33%) of the censused water objects included in the analyses. *R. arvalis* was present in all cadastre map sheets except one (05I8I; see fig 1), *B. bufo* in all except two, (07J1C and 06J5A see fig 1) and *Triturus vulgaris* in all ten map sheets. Detailed information is available in the report "Groddjur på Gotland" (Merilä et al. 2003).

## Description of the variables

*Environmental variables from the field observations*

During the visit of the water objects 12 different environmental variables were noted (TABLE 1a). Submerged vegetation was estimated in five categories 0-4, 0: no vegetation, 4 bottom completely covered with water plants. Floating vegetation was estimated as percentage coverage of the surface. Surface crossing vegetation was estimated as percentage, where 100 percent did not leave any visible surface mirror of the water between the plants. Average water depth 1: visit, was the estimated mean water depth from the first visit. Maximum water depth 1: visit, was the maximal estimated water depth from the first visit. Water level change, the estimated change of the depth from the first to the second visit. Average water depth 2: visit, the water depth change subtracted from the "average water depth 1: visit". Maximum water depth 2: visit, the water depth change subtracted from the "maximum water depth 1: visit", all water level measurements were continuous. Dried water objects were objects that dried up during the census period (binary: dried or not dried). Shadowy shoreline was estimated as percentage. In 100 percent, the sun did not reach any part of the shoreline, meaning complete canopy coverage around the object, with trees higher than the diameter of the water area. Shallow shore, was defined as the percentage proportion of the shore that 0.5 meter out from the water's edge was less than 0.1 meter deep. The environmental variables could be important indicators of physical factors such as local climate (shadow), water object morphology (shallow shore), vegetation structure (vegetation types), and water permanence.

*Variables calculated by MapInfo*

"Logarithm Area" (TABLE 1a), all the water objects that were not defined as waterlines in the cadastre map system, and were therefore not available in digital format, were digitized by hand in the program MapInfo. The program calculated all the water object areas, with exception for ditches. Ditch areas were calculated by multiplication of the width (estimated from field observations) with the ditch length (from the GIS data).

*Water object classification*

The following 11 variables (TABLE 1b) are describing the characters of the water objects as binary variables (0 / 1). It is important to point out that the same water object can be classified into maximum three different classes in the analyses. The same object could be classified as a "plant community", as a "water type" (from field classification) and a "marsh type" (from GIS classification). The most important classification comes from the field observations including the most common water types (pools, watering ponds etc.) and the most common plant community types. If a water object had a marsh like classification in the field observations ("floods" or "pools") it also got classified after the marsh type that the object was defined as in the GIS. The reason why marsh type classification from the GIS system was included in the "water object analysis" was that it could aid in understanding the results from the "buffer analyses" (see below).

"Twig rush mire" and "temporary wetland" were the most common plant communities in the censused objects (see introduction). The most common water types were "watering ponds", "cattle ponds", "open cast", "pools" and "floods". "Watering ponds" are human-made water reservoirs situated in the agricultural areas. They are normally built by soil walls, which make them deep with a steep shoreline. Special types of "cattle ponds" (brya) are also human-made and very common, and occur in all lands that are used or have been used for grazing (except agricultural land that has been changed over to pasture). These are characteristically small and very deep, with steep shorelines and placed in shadowy parts of the pasture. "Open cast" is all kind of water filled pits that are the results of human quarrying like gravel pits and peat cutting holes. "Pools" are all natural water objects with a permanent character, smaller than one hectare (more than one hectare is defined as lake). "Flood" is a shallow water object that dries up early in the season, this is normally indicated by dominance of plants characteristic for drier habitats (e.g. different species of *Poaceae*). Objects defined as other water types like "Lakes", "Bays" or "well mires" were too few in numbers to be useful in the analyses, these water objects did therefore not got any water classification at al.

Four types of marshes were defined at the cadastre maps GIS system: "marsh drier open", open marshland that is drier (defined in the GIS system as normally traversable to man, code: NOÖ). "Marsh drier coniferous" drier marshy coniferous forest (defined in the GIS system as normally traversable to man, code: NOB). "Marsh wetter open", open wetter marshland (defined in the GIS system as difficult to traverse to man, code: SVÖ). "Marsh Limy other Open", where "Limy" is the translation of blekvät, the unique Gotlandic marsh type (se introduction), other open indicate its variation in wetness (variation in traversability to man in the GIS system, code: BVÖ). If a water object contained more than one marsh type the object got classified according to the types that was characteristic to the object. This was mainly wetness, all objects containing "marsh wetter open" therefore got this classification, and all objects containing "marsh limy open" (except those containing "marsh wetter open") got this classification. The objects containing both "marsh drier coniferous" and "marsh drier open" got classified as "marsh drier coniferous" (only seven objects). The rest were defined as "marsh drier open" (the most common marsh type).

*Vegetation variables*
The vegetation of the water objects was described by seven plant species (TABLE 1c). "*Caldium mariscus*" (twig rush) is one of the most common aquatic plants on Gotland, it's distribution was therefore estimated as percentage coverage where 100 percent did not leave any visible surface mirror of the water between the plants. The other vegetation variables "*Scirpus tabernaemontani / Schoenoplectus lacustris*" (rush), "*Lemna ssp*" (duckweed), "*Typha ssp*" (reed mace) and "*Phragmites australis*" (common read), "*Carex ssp*" (sedge) and "*Chara ssp*" were just noted as present or absent since they are relatively uncommon on

Gotland. The vegetation variables could in addition to their physical structure be important indicators of the water quality.

*Fauna variables*

The fauna in the water objects was described by nine animal species (TABLE 1d). In "*Rana arvalis*" the number of spawn clumps was censused, since one female lays one spawn clump (Loman 1996) the number corresponds to the number of females in the population. In "*Bufo bufo*" the number of spawn strings was estimated in categories mainly because it is not possible to separate the strings as they often are entangled in vegetation.

The strings were therefore classified in five categories (0-4), absent; occasional (1-4); few (5-9); more (10-49) and many (>50). *B. bufo* can spawn in deeper areas far out from the shorelines, therefore also adults were noted and estimated in the same way as the spawn strings. "*Triturus vulgaris*" was estimated as the number of adults. Absolute population estimation would need a capture-recapture method or drift fence, which were impossible to arrange. A classification scale based on the number of observed adults, give at least an idea of the relative abundance in the water object. Five categories (0-4) were used: absent; occasional (1-4); few (5-9); more (10-49) and many (>50). "*Pungitius pugitius / Gasterosteus aculetus*" (sticklebacks), were also estimated in categories. Since laboratory experiments (Laurila et al. 2002) and field studies (Malmgren 2001) indicated that they have a negative influence on some amphibians and it is a common fish in smaller water objects, it was of interest to get a relative population estimate. Five categories (0-4) were used: absence; occasional (1-4); few (5-9); more (10-49) and many (>50). Other fish, "*Hirundo medicinalis*" (Medical leech), "*Haemopsis sanguisuga*" (Horse leech) and "*Dytiscus marginalis*" (diving beetles) were just noted as present or absent (0 / 1). All noted invertebrates and fishes are known predators of the three examined amphibians (Lardner and Sindenmark 1996, Fog et al. 1997, Fontaneto et al. 1998, Kuzmin 1999, Merilä and Sterner 2002) and the two anurans are potential competitors. The fauna variables are therefore expected to have a negative influence on the examined amphibians.

TABLE 1a). Environmental variables noted during the census

| Variables | Interval | unit |
|---|---|---|
| Logarithm Area | Continuous | Log square meter |
| Submerged vegetation | 0 – 4 | Categories |
| Floating vegetation | 0 – 100 | Percentage |
| Surface crossing vegetation | 0 – 100 | Percentage |
| Average water depth 1: visit | Continuous | Meter |
| Maximum water depth 1: visit | Continuous | Meter |
| Water depth change | Continuous | Meter |
| Average water depth 2: visit | Continuous | Meter |
| Maximum water depth 2: visit | Continuous | Meter |
| Dried water objects | 0 / 1 | Binary |
| Shadowy shoreline | 0 – 100 | Percentage |
| Shallow shoreline | 0 – 100 | Percentage |

TABLE 1b). Water classification variables from GIS system and noted during the census

| Variables | interval | Unit |
|---|---|---|
| Twig rush mire (agmyr) | 0 / 1 | Binary |
| Temporary wetland (vät) | 0 / 1 | Binary |
| Watering pond | 0 / 1 | Binary |
| Cattle pond | 0 / 1 | Binary |
| Open cast | 0 / 1 | Binary |
| Pool | 0 / 1 | Binary |
| Flood | 0 / 1 | Binary |
| Marsh limy open | 0 / 1 | Binary |
| Marsh drier coniferous | 0 / 1 | Binary |
| Marsh drier open | 0 / 1 | Binary |
| Marsh wetter open | 0 / 1 | Binary |

TABLE 1c). Vegetation variables noted during the census

| Variable | Interval | unit |
|---|---|---|
| *Caldium mariscus* | 0 – 100 | Percentage |
| *Scirpus tabernaemontani / Schoenoplectus lacustris* | 0 / 1 | Binary |
| *Lemna ssp* | 0 / 1 | Binary |
| *Carex ssp* | 0 / 1 | Binary |
| *Typha ssp* | 0 / 1 | Binary |
| *Phragmites australis* | 0 / 1 | Binary |
| *Chara ssp* | 0 / 1 | Binary |

TABLE 1d). Fauna variables noted during the census

| Variables | Interval | Unit |
|---|---|---|
| *Rana arvalis* | Continuous | # Spawn clumps |
| *Bufo bufo spawn strings* | 0 – 4 | Categories |
| *Bufo bufo adults* | 0 – 4 | Categories |
| *Triturus vulgaris* | 0 – 4 | Categories |
| *Pungitius pugitius / Gasterosteus aculetus* | 0 – 4 | Categories |
| Other fish | 0 / 1 | Binary |
| *Hirundo medicinalis* | 0 / 1 | Binary |
| *Haemopsis sanguisuga* | 0 / 1 | Binary |
| *Dytiscus marginalis* | 0 / 1 | Binary |

*Landscape variables from cadastre maps*

The GIS variables of the censused areas were taken from two maps (TABLE 2), one cadastre map from 2001, (scale 1:10000) and one cadastre map from the end of 17:th to the beginning of the 18:th-century, depending on the region (scale 1:10000). The number of square meters was calculated for all the variables available from the two maps on one square kilometre scale.

From the cadastre map 2001, buffers of two widths, 500 and 1000-m around all water objects were created and the number of square meters of each variable was calculated. All calculations of the GIS variables were made in the program MapInfo (MapInfo, New York, USA, www.mapinfo.com).

TABLE 2. Variables available from the cadastre maps of 21:th and 18:th century respectively

| Variables | Map 21:th | Map 18:th |
|---|---|---|
| Agriculture | X | X |
| Open land | X | |
| Deciduous forest | X | |
| Coniferous forest | X | |
| Cut forest | X | |
| Marsh limy open | X | |
| Marsh drier coniferous | X | |
| Marsh drier open | X | |
| Marsh wetter open | X | |
| Sea | X | |
| Water surface | X | |
| Lake | | X |
| Meadow | | X |
| Pasture | | X |
| Mire | | X |

*Preparation of the data*

As it is important to avoid skew distribution of the data in the statistical analyses, the "Area" of the water objects was log transformed. For the same reason the proportion of the different GIS variables was converted from absolute proportion ($m^2$) to relative proportions (%) of the buffer area. The advantage of a relative proportion is that the correlation between buffer size and the effect on the variables disappears.

The variable "*B. bufo*" was a combination of two variables, estimated "*B. bufo* eggstrings" and estimated "number of *B. bufo* adults". The "number of adults" gives a week indication of the population size but indicates presence when no eggstrings were found. The only difference between "*B. bufo*" and "*B. bufo* eggstrings" is that "*Bufo bufo*" had all objects with presence of adults but no observations of eggstrings classified to 1; equal with estimation of 1-4 eggstrings, for indicating presence. The assumption was that if *B. bufo* is present in a water object at springtime it is a likely breeding site.

## Statistical methods

*Habitat analyses: stepwise multiple logistic regressions*

The statistical method applied was stepwise multiple logistic regression in the BMDP software (BMDP 1992). The dependent variable in logistic regression is binary (example: presence/absence of frogs in a pond) and the independent variables could be binary, categorical or continuous. The main advantage with multiple logistic regression is the possibility to combine continuous and categorical independent variables in the same analysis and the data does not have to be normally distributed (Hosmer and Lemeshow 1989).

The program starts with all independent variables outside the model. The independent variables are tested with an approximate chi square test, and the variable that best discriminates between presence and absence of the dependent variable (had the lowest $P$ value and highest $\chi^2$ value) is stepped in to the model. The same procedure is then repeated for the variables left outside. The program is iterating values on the constant $\beta_0$ and the regression coefficient $\beta_1$ to minimise the difference between the calculated and observed probability of presence. All variables left in the model have a relative significance in explaining presence, which strength is indicated by a $P$-value (normally $< 0.10$) and importance by a $\chi^2$ value (higher $\chi^2$ value indicates that the variable have greater influence on the model). These two values ($P$ and $\chi^2$) gives therefore information about the relative importance that the single variables have on the whole model. The program also calculates regression coefficient ($\beta$) for the significant variables, which indicates if the variables have a negative or positive influence on the dependent variable. The significance of the model is given by a "goodness of fit" value, measured as a deviance - $\chi^2$ where a low $\chi^2$ value and a high $P$-value (0 - 1) give a high agreement between the model and observations (Hosmer and Lemeshow 1989, Dixon 1992).

The $P$-value can therefore mean *two* completely different things, depending on the question. The probability of deviation from random, where a low $P$-value indicates that the results are not caused by a random effect (the level is normally put at $P < 0.10$ when many independent variables are tested on one dependent variable). It can also mean that the probability of agreement between the model and observations is high; a high $P$-value – high agreement (1 = 100%).

The two main variable groups, buffer data (from the geographical information system) and water object data (mainly from the census) were divided into several subgroups with around ten variables in each.

The buffers were of two kinds (500 and 1000 meters around the objects respectively) and were analysed separately. To investigate the influence of the surrounding GIS variables and to see if the variables affected the species differently on 500 respectively 1000 meters scales, all GIS variables that had a significant influence ($P<0.10$) were analysed together in a "combined model".

The water object variables were grouped into environmental, water classification, vegetation and fauna variables. First they were all analysed separately, and then together in a combined model with the following design: the environmental and vegetation variables that had significant influence (positive or negative) on the occurrence of the species ($P<0.10$), and the fauna variables that had a significant negative influence. This was done in order to build a model that best fitted the observations and find out which variables that had the greatest importance in explaining occurrence of the analysed amphibians. Significant positive associations between the fauna variables and the analysed amphibians were assumed to be non-causal, since the observed fauna variables are not important prey of the analysed amphibians (Fog et al. 1997). Some of the fauna variables are known to have similar habitat preference as the amphibians and could therefore "hide" important causal variables if they got included in the combined analyses (Nilsson 1998).

*Land use change analysis: univariate tests*

Most of the anthropogenic water objects like cattle ponds, open casts and watering ponds did probably not exist 300 years ago. The few wetlands left today were probably much larger and deeper during the 18:th-century since ditching during the 20:th-century has effected most of them. To make buffers on the cadastre map from the 18:th-century around the water objects that were found in the census from the 21:th-century would therefore give a false view. But it is possible to compare the change in distribution of agricultural land between kilometre squares with presence and absence of amphibians. Information about the distribution of agricultural area is available from both maps. The increase of agricultural land (defined as the "agricultural expansion") was probably proportional to the decrease of wetlands, and could therefore give a picture of the decrease in amphibian habitats during the past 300 years. The difference in median value of agricultural expansion in square kilometres with presence and absence of each amphibian species were therefore analysed by a Mann-Whitney U-test. Since occurrence of amphibians is related to occurrence of water objects the difference in "agricultural expansion" between square kilometres with presence and absence of water objects was also analysed. The Mann-Whitney U-tests were made by the JMP software (SAS 2000).

# Results

## Water object analyse: logistic regression

*Rana arvalis*

"Shadowy shore" (negative association), "log area" and "submerged vegetation" (positive association) had significant associations with the presence of *R. arvalis* and entered into the environmental model (TABLE 3a). The Goodness of fit for this model was $P = 0.725$. "Pool" (positive) and "cattle pond" (negative) were the only variables that fitted in the water object classification model (goodness of fit $P < 0.0001$, TABLE 3b). The model for vegetation variables ended up with "*C. mariscus*", "*Cara ssp*", and "*Carex ssp*", all with a positive association with the presence of *R. arvalis*, (goodness of fit $P = 0.003$, TABLE 3c). In the fauna model "*B. Bufo*", "*T. vulgaris*", "other fish" and "*H. sanguisuga*" were entered (goodness of fit $P = 0.006$, TABLE 3d). All had a positive association with presence of *R. arvalis*. The combined model, a combination of the significant environmental and vegetation variables, and negatively associated fauna (none), resulted in "shadowy shore", "log area", "*Carex ssp*", "*C. mariscus*" and "*Chara ssp*", the goodness of fit was $P = 0.884$ for the model (TABLE 3e).

TABLE 3. Results of stepwise logistic regression: water object analyses for the presence of *R. arvalis*. The mean value and standard deviation is given for the variables in water objects with presence and absence of *R. arvalis* respectively. The "coefficient" (β-value), probability (*P*-value) and chi-square ($\chi^2$-value) is given for all variables that fitted the model ($P < 0.10$). The "coefficient" indicates if the correlation is positive or negative, the *P*-values give the significance level and the $\chi^2$-values the contribution that each of the variables gives to the goodness of fit value for the whole model.

TABLE 3a). *Environmental model for R. arvalis*

| | Mean ± SD | | | | |
|---|---|---|---|---|---|
| Variables | Presence | Absence | Coeff (β)±SE | $\chi^2$ | *P* |
| Shallow shore | 57±40 | 54±42 | | | >0.10 |
| Floating vegetation | 1.5±5.3 | 1.8±6.1 | | | >0.10 |
| Surface crossing vegetation | 34±32 | 18±27 | | | >0.10 |
| Average w depth 1:v | 0.35±0.24 | 0.42±0.34 | | | >0.10 |
| Maximum w depth 1: v | 0.74±0.39 | 0.71±0.48 | | | >0.10 |
| Water depth change | -0.02±0.06 | -0.03±0.08 | | | >0.10 |
| Average w depth 2: v | 0.33±0.26 | 0.38±0.36 | | | >0.10 |
| Maximum w depth 2: v | 0.71±0.40 | 0.68±0.50 | | | >0.10 |
| Dried w objects | 0 | 0.02±0.13 | | | >0.10 |
| Shadowy shore | 13±17 | 27±30 | -0.02±0.01 | 77 | 0.000 |
| Log Area | 8.8±1.6 | 6.6±2.6 | 0.53±0.09 | 40 | 0.000 |
| Submerge vegetation | 1.2±1.0 | 0.8±1.1 | 0.44± 0.13 | 11 | 0.001 |

Goodness of fit: $\chi^2 = 296$, $P = 0.725$.

TABLE 3b). *Water classification model for R. arvalis*

| Variables | Mean ± SD Presence | Absence | Coeff (β)±SE | $\chi^2$ | *P* |
|---|---|---|---|---|---|
| Twig rush mire (agmyr) | 0.26±0.44 | 0.12±0.33 | | | >0.10 |
| Temporary wetland (vät) | 0.21±0.41 | 0.23±0.42 | | | >0.10 |
| Watering pond | 0.08±0.27 | 0.1±0.30 | | | >0.10 |
| Open cast | 0.12±0.32 | 0.12±0.32 | | | >0.10 |
| Flood | 0.15±0.36 | 0.20±0.40 | | | >0.10 |
| Marsh limy open | 0.27±0.45 | 0.18±0.38 | | | >0.10 |
| Marsh drier coniferous | 0.04±0.19 | 0.01±0.11 | | | >0.10 |
| Marsh drier open | 0.34±0.48 | 0.28±0.45 | | | >0.10 |
| Marsh wetter open | 0.16±0.36 | 0.06±0.23 | | | >0.10 |
| Pool | 0.57±0.50 | 0.29±0.50 | 0.95±0.27 | 20 | 0.000 |
| Cattle pond | 0.02±0.15 | 0.17±0.38 | -1.71±0.75 | 8 | 0.005 |

Goodness of fit: $\chi^2 = 71$, $P < 0.0001$.

TABLE 3c). *Vegetation model for R. arvalis*

| Variables | Mean ± SD Presence | Absence | Coeff (β)±SE | $\chi^2$ | *P* |
|---|---|---|---|---|---|
| *S. tabernaemontani / S. lacustris* | 0.06±0.24 | 0.03±0.17 | | | >0.10 |
| *Lemna ssp* | 0.012±0.11 | 0.03±0.16 | | | >0.10 |
| *Typha ssp* | 0.19±0.38 | 0.13±0.33 | | | >0.10 |
| *P. australis* | 0.20±0.40 | 0.09±0.29 | | | >0.10 |
| *Chara ssp* | 0.43±0.50 | 0.13±0.34 | 1.23±0.31 | 29 | 0.000 |
| *C. mariscus* | 34±34 | 13±26 | 0.02±0.00 | 18 | 0.000 |
| *Carex ssp* | 66±0.48 | 0.35±0.48 | 1.05±0.29 | 14 | 0.000 |

Goodness of fit: $\chi^2 = 126$, $P = 0.003$.

TABLE 3d). *Fauna model for R. arvalis*

| Variables | Mean ± SD Presence | Absence | Coeff (β)±SE | $\chi^2$ | *P* |
|---|---|---|---|---|---|
| *P. pugitius / G. aculetus* | 0.16±0.53 | 0.05±0.32 | | | >0.10 |
| *H. medicinalis* | 0.02±0.15 | 0.004±0.07 | | | >0.10 |
| *D. marginalis* | 0.01±0.11 | 0.01±0.09 | | | >0.10 |
| *B. bufo* | 1.4±1.5 | 0.46±1.0 | 0.43±0.10 | 31 | 0.000 |
| *T. vulgaris* | 0.73±0.78 | 0.32±0.67 | 0.63±0.18 | 12 | 0.000 |
| Other fish | 0.07±0.26 | 0.022±0.15 | 1.20±0.69 | 3 | 0.090 |
| *H. sanguisuga* | 0.16±0.36 | 0.04±0.19 | 0.84±0.51 | 3 | 0.098 |

Goodness of fit: $\chi^2 = 69$, $P = 0.006$.

TABLE 3e). *Combined model for R. arvalis, all variables that fit in the models above, except positive fauna*

| Variables | Coeff (β)±SE | $\chi^2$ | *P* |
|---|---|---|---|
| Cattle pond | | | >0.10 |
| Pool | | | >0.10 |
| Submerged vegetation | | | >0.10 |
| Shadowy shore | -0.2±0.01 | 77 | 0.000 |
| Log Area | 0.35±0.14 | 40 | 0.000 |
| Carex ssp | 1.03±0.31 | 16 | 0.000 |
| Chara ssp | 0.89±0.51 | 7 | 0.006 |
| C. mariscus | 0.2±0.01 | 3 | 0.056 |

Goodness of fit: $\chi^2 = 280$, $P = 0.884$.

*Bufo bufo*
"Shadowy shore" (negative association), "log area" (positive association), "submerged vegetation" (positive association) and "Floating vegetation" (negative) had a significant association with the presence of *B. bufo* and entered the model of the environmental variables, the goodness of fit was $P = 0.172$ (TABLE 4a). The variables that entered the water classification model were "marsh limy open" and "twig rush mire", both positive and "cattle pond" that was negative, (goodness of fit $P = 0.134$, TABLE 4b). The model for vegetation variables ended up with "*C. mariscus*", "*Cara ssp*", "*Lemna ssp*" and "*P. australis*", all except "*Lemna ssp*" had a positive association with presence of *B. bufo*, (goodness of fit $P = 0.079$, TABLE 4c). The high standard error for the coefficient of "*Lemna ssp*" ($1.79*10^{18}$) was probably caused by the askew distribution of the variable, "*Lemna ssp*" was only found in seven water objects and non of them contained *B. bufo* (Appendix 2). In the fauna model "*R. arvalis*", "*T. vulgaris*" and "*H. sanguisuga*" were entered (goodness of fit $P = 0.001$, TABLE 4d). All had a positive association with presence of *B. bufo*. The combined model resulted in, "shadowy shore", "log area", "submerge vegetation", "floating vegetation", "marsh limy open" and "*Lemna ssp*" (Goodness of fit $P = 0.210$, TABLE 4d). The program found that 100 iterations was not enough to satisfy the convergence criteria, but increasing the number of iterations did not help.

TABLE 4. Results of stepwise logistic regression water object analyses, for the presence of *B. bufo*. The mean value and standard deviation is given for the variables in the water objects with presence and absence of *B. bufo* respectively. The "coefficient" (β-value), probability (*P*-value) and chi-square ($\chi^2$-value) is given for all variables that fitted the model ($P < 0.10$). The "coefficient" indicates if the correlation is positive or negative, the *P*-values give the significance level and the $\chi^2$-values the contribution that each of the variables give to the goodness of fit value for the whole model.

TABLE 4a). *Environmental model for B. bufo*

| Variables | Mean ± SD Presence | Mean ± SD Absence | Coeff(β)±SE | $\chi^2$ | P |
|---|---|---|---|---|---|
| Shallow shore | 59±40 | 53±42 | | | >0.10 |
| Surface crossing vegetation | 29±34 | 19±27 | | | >0.10 |
| Average w depth 1: v | 0.40±0.32 | 0.40±0.32 | | | >0.10 |
| Maximum w depth 1: v | 0.76±0.47 | 0.70±0.45 | | | >0.10 |
| W depth change | -0.02±0.07 | -0.04±0.09 | | | >0.10 |
| Dried w objects | 0 | 0.02±0.13 | | | >0.10 |
| Average water depth 2: v | 0.37±0.34 | 37±0.34 | | | >0.10 |
| Maximum water depth 2: v | 0.73±0.48 | 0.67±0.47 | | | >0.10 |
| Shadowy shore | 14±18 | 27±31 | -0.20±0.01 | 54 | 0.000 |
| Log area | 8.5±1.8 | 6.6±2.6 | 0.38±0.08 | 24 | 0.000 |
| Submerged vegetation | 1.2±1.1 | 0.77±1.07 | 0.53± 0.13 | 13 | 0.000 |
| Floating vegetation | 1.0±4.2 | 2.0±6.5 | -0.06±0.03 | 5 | 0.023 |

Goodness of fit: $\chi^2 = 333$, $P = 0.172$.

TABLE 4b). *Water classification model for B. bufo*

| | Mean ± SD | | | | |
|---|---|---|---|---|---|
| Variables | Presence | Absence | Coeff (β)±SE | $\chi^2$ | *P* |
| Temporary wetland (vät) | 0.24±0.43 | 0.22±0.42 | | | >0.10 |
| Watering pond | 0.10±0.29 | 0.10±0.30 | | | >0.10 |
| Open cast | 0.13±0.34 | 0.11±0.32 | | | >0.10 |
| Flood | 0.20±0.40 | 0.18±0.38 | | | >0.10 |
| Pool | 0.46±0.50 | 0.32±0.47 | | | >0.10 |
| Marsh drier coniferous | 0.02±0.14 | 0.02±0.13 | | | >0.10 |
| Marsh wetter open | 0.09±0.29 | 0.08±27 | | | >0.10 |
| Marsh drier open | 0.33±0.47 | 0.29±0.45 | | | >0.10 |
| Cattle pond | 0.06±0.24 | 0.17±0.37 | -0.89±0.47 | 8 | 0.006 |
| Marsh limy Open | 0.29±0.46 | 0.16±0.37 | 0.62±0.29 | 5 | 0.030 |
| Twig rush mire | 0.23±0.42 | 0.12±0.33 | 0.59±0.32 | 3 | 0.069 |

Goodness of fit: $\chi^2 = 44$, $P = 0.134$.

TABLE 4c). *Vegetation model for B. bufo*

| | Mean ± SD | | | | |
|---|---|---|---|---|---|
| Variables | Presence | Absence | Coeff (β)±SE | $\chi^2$ | *P* |
| *Carex ssp* | 0.53±0.50 | 0.38±0.49 | | | >0.10 |
| *S. tabernaemontani / S. lacustris* | 0.06±0.24 | 0.028±0.16 | | | >0.10 |
| *Typha ssp* | 0.11±0.32 | 0.15±0.36 | | | >0.10 |
| *Chara ssp* | 0.36±0.48 | 0.14±0.35 | 1.03±0.30 | 19 | 0.000 |
| *C. mariscus* | 28±34 | 14±27 | 0.01±0.00 | 8 | 0.005 |
| *Lemna ssp* | 0 | 0.03±0.18 | $-199\pm1.79*10^{18}$ | 5 | 0.021 |
| *P. australis* | 0.18±0.39 | 0.09±0.29 | 0.68±0.38 | 3 | 0.073 |

Goodness of fit: $\chi^2 = 0.079$, $P = 104$.

TABLE 4d). *Fauna model for B. bufo*

| | Mean ± SD | | | | |
|---|---|---|---|---|---|
| Variables | Presence | Absence | Coeff (β)±SE | $\chi^2$ | *P* |
| Other fish | 0.06±0.24 | 0.02±0.15 | | | >0.10 |
| P. pugitius / G. aculetus | 0.15±0.50 | 0.05±0.32 | | | >0.10 |
| H. medicinalis | 0.14±0.35 | 0.04±0.19 | | | >0.10 |
| D. marginalis | 0.02±0.14 | 0.005±0.07 | | | >0.10 |
| R. arvalis | 35±117 | 5.0±19 | 0.02±0.00 | 25 | 0.000 |
| H. sanguisuga | 0.14±0.35 | 0.04±0.19 | 1.11±0.49 | 7 | 0.010 |
| T. vulgaris | 0.63±0.77 | 0.33±0.68 | 0.38±0.17 | 5 | 0.027 |

Goodness of fit: $\chi^2 = 127$, $P = 0.001$.

TABLE 4e). Combined model for *B. bufo*, all variables that fit in the models above, except positive fauna

| Combination of variables ($P$<0.1) | Coeff (β)±SE | $\chi^2$ | $P$ |
|---|---|---|---|
| P. australis | | | >0.10 |
| Chara ssp | | | >0.10 |
| Cattle pond | | | >0.10 |
| C. mariscus | | | >0.10 |
| Twig rush mire | | | >0.10 |
| Shadowy shore | -0.02±0.01 | 54 | 0.000 |
| Log area | 0.36±0.08 | 16 | 0.000 |
| Submerged vegetation | 0.54±0.13 | 7 | 0.007 |
| Lemna ssp | $-296.7\pm1.79*10^{19}$ | 4 | 0.039 |
| Floating vegetation | -0.05±0.03 | 3 | 0.060 |
| Marsh limy open | 0.53±0.32 | 3 | 0.096 |

Goodness of fit: $\chi^2 = 327$, $P = 0.210$.

*Triturus vulgaris*

"Shadowy shore", "average w depth 1: v" and "dried w objects" had negative, and "submerged vegetation" had positive association with the presence of *T vulgaris* and entered the model of the environmental variables, the goodness of fit was $P = 0.009$ (TABLE 5a). The high standard error for the coefficient of "dried w objects" ($2.36*10^{20}$) was probably caused by the askew distribution of the variable since only four water objects dried during the censused period, and no one of them contained *T. vulgaris* (Appendix 2). "Pool" (positive) and "watering pond" (negative) were the variables that best fitted in the water classification model (goodness of fit $P$ =0.314, TABLE 5b). The model for vegetation variables ended up with "*C. mariscus*", "*Cara ssp*", "*Carex ssp*" and "*S. tabernaemontani / S. lacustris*", all except "*S. tabernaemontani / S. lacustris*" had a positive association with presence of *T. vulgaris*, (goodness of fit $P = 0.002$, TABLE 5c). In the fauna model "*R. arvalis*", "*B. bufo*", "*H. sanguisuga*" "other fish" and "*D. marginalis*" was entered (goodness of fit $P = 0.036$). All had a positive association except "other fish"(TABLE 5c). The high standard error for the coefficient of "*D. marginalis*" ($2.73*10^{18}$) was probably caused by the askew distribution of the variable, "*D. marginalis*" was only found in three water objects and no one of them contained *T. vulgaris* (Appendix 2). Left in the final model (combination of variables from the environmental, water classification, vegetation models, and the negative fauna variables), were watering pond, pool, *Chara ssp*, other fish, *Carex ssp* and *S. tabernaemontani / S. lacustris* the goodness of fit was $P = 0.059$ (TABLE 5e).

TABLE 5. Results of stepwise logistic regression, water object analyses for the presence of *T. vulgaris*. The mean value and standard deviation is given for the variables in the water objects with presence and absence of *T. vulgaris* respectively. The "coefficient" (β-value), probability (*P*-value) and chi-square ($\chi^2$-value) is given for all variables that fitted the model ($P < 0.10$). The "coefficient" indicates if the correlation is positive or negative, the *P*-values give the significance level and the $\chi^2$-values the contribution that each of the variables give to the goodness of fit value for the whole model.

TABLE 5a). *Environmental model for T. vulgaris*

| | Mean ± SD | | | | |
|---|---|---|---|---|---|
| Variables | Presence | Absence | Coeff (β)±SE | $\chi^2$ | *P* |
| Log Area | 7.9±2.2 | 6.9±2.7 | | | >0.10 |
| Shallow shore | 63±38 | 50±43 | | | >0.10 |
| Floating vegetation | 1.2±4.3 | 1.9±6.5 | | | >0.10 |
| Surface crossing vegetation | 29±31 | 18±28 | | | >0.10 |
| W depth change | -0.02±0.06 | -0.04±0.09 | | | >0.10 |
| Maximum w depth 2: v | 0.66±0.42 | 0.70±0.50 | | | >0.10 |
| Average w depth 2: v | 0.30±0.22 | 0.40±0.38 | | | >0.10 |
| Maximum w depth 1: v | 0.68±0.42 | 0.74±0.47 | | | >0.10 |
| Average w depth 1: v | 0.32±0.22 | 0.44±0.35 | -1.75±0.41 | 45 | 0.000 |
| Shadowy shore line | 17±21 | 26±31 | -0.01±0.00 | 7 | 0.007 |
| Submerge vegetation | 1.1±1.1 | 0.8±1.1 | 0.30± 0.11 | 8 | 0.004 |
| Dried w objects | 0 | 0.019±0.14 | $-9.99\pm2.36*10^{20}$ | 4 | 0.047 |

Goodness of fit: $\chi^2 = 373$, $P = 0.009$.

TABLE 5b). *Water classification model for T. vulgaris*

| | Mean ± SD | | | | |
|---|---|---|---|---|---|
| Variables | Presence | Absence | Coeff (β)±SE | $\chi^2$ | *P* |
| Twig rush mire | 0.23±0.42 | 0.12±0.33 | | | >0.10 |
| Temporary wetland | 0.23±0.42 | 0.23±0.42 | | | >0.10 |
| Cattle pond | 0.08±0.27 | 0.16±0.37 | | | >0.10 |
| Open cast | 0.10±0.31 | 0.12±0.33 | | | >0.10 |
| Flood | 0.16±0.37 | 0.19±0.40 | | | >0.10 |
| Marsh limy open | 029±0.45 | 0.16±0.37 | | | >0.10 |
| Marsh drier coniferous | 0.01±0.98 | 0.02±0.15 | | | >0.10 |
| Marsh drier open | 0.39±0.49 | 0.26±0.44 | | | >0.10 |
| Marsh wetter open | 0.09±0.28 | 0.08±0.27 | | | >0.10 |
| Pool | 0.59±0.49 | 0.25±0.43 | 1.33±0.26 | 35 | 0.000 |
| Watering pond | 0.019±0.14 | 0.13±0.34 | -1.47±0.75 | 5 | 0.020 |

Goodness of fit: $\chi^2 = 40$, $P = 0.314$.

TABLE 5c). *Vegetation model for T. vulgaris*

| | Mean ± SD | | | | |
|---|---|---|---|---|---|
| Variables | Presence | Absence | Coeff (β)±SE | $\chi^2$ | *P* |
| *Lemna ssp* | 0.01±0.1 | 0.03±0.17 | | | >0.10 |
| *Typha ssp* | 0.11±0.32 | 0.15±0.36 | | | >0.10 |
| *P. australis* | 0.11±0.32 | 0.12±0.33 | | | >0.10 |
| *Chara ssp* | 0.35±0.48 | 0.14±0.35 | 0.91±0.30 | 17 | 0.000 |
| *C. mariscus* | 28±34 | 14±27 | 0.01±0.00 | 8 | 0.004 |
| *Carex ssp* | 0.57±0.50 | 0.36±0.48 | 0.70±0.26 | 7 | 0.009 |
| *S. tabernaemontani / S. lacustris* | 0.019±0.14 | 0.048±0.21 | -1.58±0.82 | 5 | 0.028 |

Goodness of fit: $\chi^2 = 127$, $P = 0.002$.

TABLE 5d). *Fauna model for T. vulgaris*

| | Mean ± SD | | | | |
|---|---|---|---|---|---|
| Variables | Presence | Absence | Coeff (β)±SE | $\chi^2$ | *P* |
| *P. pugitius / G. aculetus* | 0.10±0.46 | 0.067±0.35 | | | >0.10 |
| *H. medicinalis* | 0.019±0.14 | 0.005±0.69 | | | >0.10 |
| *B. bufo* | 1.2±1.48 | 0.47±1.05 | 0.38±0.11 | 22 | 0.000 |
| *R. arvalis* | 33±114 | 5±19 | 0.02±0.01 | 14 | 0.000 |
| Other fish | 0.010±0.10 | 0.05±0.21 | -3.13±0.21 | 11 | 0.001 |
| *D. marginalis* | 0.028±0.17 | 0 | $199.9\pm2.73*10^{18}$ | 5 | 0.019 |
| *H. sanguisuga* | 0.14±0.35 | 0.033±0.18 | 1.08±0.534 | 4 | 0.039 |

Goodness of fit: $\chi^2 = 112$, $P = 0.036$.

TABLE 5e). *Combined model for T. vulgaris, all variables that fit in the models above, except positive fauna*

| Variables | Coeff (β)±SE | $\chi^2$ | *P* |
|---|---|---|---|
| Submerged vegetation | | | >0.10 |
| Average w depth 1: v | | | >0.10 |
| Dried w objects | | | >0.10 |
| Shadowy shore | | | >0.10 |
| C. mariscus | | | >0.10 |
| Chara ssp | 1.00±0.32 | 6 | 0.013 |
| Pool | 0.94±0.28 | 7 | 0.010 |
| Other fish | -1.82±1.14 | 4 | 0.060 |
| Watering pond | -1.48±0.76 | 16 | 0.000 |
| Carex ssp | 0.53±0.28 | 3 | 0.077 |
| *S. tabernaemontani / S. lacustris* | -1.4±0.85 | 3 | 0.075 |

Goodness of fit: $\chi^2 = 315$, $P = 0.059$.

TABLE 6. Comparison of the stepwise logistic results (goodness of fit value) of field variables between the three amphibians

| Model | Fit *Rana arvalis (P)* | Fit *Bufo bufo (P)* | Fit *Triturus vulgaris (P)* |
|---|---|---|---|
| Environmental | 0.725 | 0.172 | 0.009 |
| Water classification | 0.000 | 0.134 | 0.314 |
| Vegetation | 0.003 | 0.079 | 0.002 |
| Fauna | 0.006 | 0.001 | 0.036 |
| Combination | 0.884 | 0.210 | 0.059 |

## Landscape analysis of buffer variables: logistic regression

*Rana arvalis*

The percentage proportion of "agriculture", "sea" and "cut forest" had a significant ($P<0.10$) negative association with presence of *R. arvalis* in the 500-m width buffer. "Marsh wetter open" and "deciduous forest" had a positive association. Together they build a model with a goodness of fit at $P = 0.308$ (TABLE 7a).

In the model for the buffer of 1000-m width, only agriculture, sea and cut forest passed the significant level ($P<0.10$), all had a negative influence on *R. arvalis*. The goodness of fit was $P = 0.126$ (TABLE 7b).

The combined buffer model (combination of the significant variables from the two models above) ended up with exactly the same variables and goodness of fit value as the model for buffer 500-m (TABLE 7c).

TABLE 7. Results of stepwise logistic regression: buffer analyses for the presence of *R. arvalis*. The mean value and standard deviation is given for the percentage proportion of the GIS variables in buffers around water objects with presence and absence of *R. arvalis* respectively. The "coefficient" (β-value), probability (*P*-value) and chi-square ($\chi^2$-value) is given for all variables that fitted the model ($P < 0.10$). The "coefficient" indicates if the correlation is positive or negative, the *P*-values give the significance level and the $\chi^2$-values the contribution that each of the variables gives to the goodness of fit value for the whole model.

TABLE 7a). *Buffer 500-m model for R. arvalis*

| | Mean ± SD | | | | |
|---|---|---|---|---|---|
| Variables | Presence | Absence | Coeff (β)±SE | $\chi^2$ | *P* |
| Open land | 28±28 | 25±21 | | | >0.10 |
| Coniferous forest | 51±29 | 44±27 | | | >0.10 |
| Marsh limy open | 2.8±5.3 | 1.8±2.6 | | | >0.10 |
| Marsh drier coniferous | 0.49±1.4 | 0.32±1.4 | | | >0.10 |
| Marsh drier open | 1.9±3.5 | 1.3±2.9 | | | >0.10 |
| Water surface | 1.0±2.8 | 1.0±3.2 | | | >0.10 |
| Agriculture | 8.1±11 | 19±22 | -0.06±0.01 | 85 | 0.000 |
| Sea | 1.8±7.2 | 4.0±12 | -0.05±0.02 | 13 | 0.000 |
| Cut forest | 1.7±3.5 | 1.9±3.3 | -0.12±0.04 | 10 | 0.002 |
| Marsh wetter open | 1.7±4.0 | 0.4±1.5 | 0.09±0.05 | 4 | 0.058 |
| Deciduous forest | 1.2±3.8 | 0.53±2.2 | 0.09±0.05 | 3 | 0.063 |

Goodness of fit: $\chi^2 = 322$, $P = 0.308$.

TABLE 7b). *Buffer 1000-m model for R. arvalis*

| | Mean ± SD | | | | |
|---|---|---|---|---|---|
| Variables | Presence | Absence | Coeff (β)±SE | $\chi^2$ | *P* |
| Open land | 26±24 | 21±17 | | | >0.10 |
| Coniferous forest | 50±26 | 45±24 | | | >0.10 |
| Marsh limy open | 2.2±2.7 | 1.8±2.3 | | | >0.10 |
| Marsh drier coniferous | 0.39±0.90 | 0.30±0.81 | | | >0.10 |
| Marsh drier open | 1.5±2.1 | 1.0±1.8 | | | >0.10 |
| Water surface | 1.4±2.7 | 1.1±3.4 | | | >0.10 |
| Marsh wetter open | 0.89±1.8 | 0.41±1.2 | | | >0.10 |
| Deciduous forest | 1.1±2.7 | 0.67±1.8 | | | >0.10 |
| Agriculture | 10±13 | 19±20 | -0.05±0.02 | 83 | 0.000 |
| Sea | 4.7±9.7 | 6.1±15 | -0.02±0.01 | 7 | 0.006 |
| Cut forest | 2.06±3.0 | 2.02±2.5 | -0.09±0.04 | 5 | 0.022 |

Goodness of fit: $\chi^2 = 340$, $P = 0.126$.

TABLE 7c). *Combined buffer model for R. arvalis, all variables that fit in the models for buffer 500 and 1000-m.*

| Variables | Coeff (β)±SE | $\chi^2$ | *P* |
|---|---|---|---|
| Agriculture (1000) | | | >0.10 |
| Sea (1000) | | | >0.10 |
| Cut forest (1000) | | | >0.10 |
| Agriculture (500) | -0.06±0.01 | 85 | 0.000 |
| Sea (500) | -0.05±0.02 | 13 | 0.000 |
| Cut forest (500) | -0.12±0.04 | 10 | 0.002 |
| Marsh wetter open (500) | 0.09±0.05 | 4 | 0.058 |
| Deciduous forest (500) | 0.09±0.05 | 3 | 0.063 |

Goodness of fit: $\chi^2 = 322$, $P = 0.308$.

*Bufo bufo*

The percentage proportion of "agriculture", "sea" and "coniferous forest" had a significant ($P$<0.10) negative association with presence of *B. bufo*. "Marsh drier open" had a positive association. Together they build a model of variables from the 500-m width buffer that end with a goodness of fit at $P = 0.021$ (TABLE 8a).

In the model for the Buffer 1000-m width, only agriculture and sea passed the significant level ($P$<0.10), all had a negative influence on *B. bufo*. The goodness of fit was $P = 0.013$ (TABLE 8b).

The combined buffer model (combination of the significant variables from the two previous models) ended up with agriculture from Buffer 1000 and sea from buffer 500, goodness of fit $P = 0.017$ (TABLE 8c).

TABLE 8. Results of stepwise logistic regression: buffer analyses for the presence of *B. bufo*. The mean value and standard deviation is given for the percentage proportion of the GIS variables in buffers around water objects with presence and absence of *B. bufo* respectively. The "coefficient" (β-value), probability ($P$-value) and chi-square ($\chi^2$-value) is given for all variables that fitted the model ($P < 0.10$). The "coefficient" indicates if the correlation is positive or negative, the $P$-values give the significance level and the $\chi^2$-values the contribution that each of the variables gives to the goodness of fit value for the whole model.

TABLE 8a). *Buffer 500-m model for B. bufo*

| | Mean ± SD | | | | |
|---|---|---|---|---|---|
| Variables | Presence | Absence | Coeff (β)±SE | $\chi^2$ | *P* |
| Open land | 27±26 | 25±22 | | | >0.10 |
| Deciduous forest | 0.93±3.8 | 0.63±2.1 | | | >0.10 |
| Cut forest | 2.0±3.6 | 1.8±3.2 | | | >0.10 |
| Marsh limy open | 2.5±4.8 | 1.8±2.7 | | | >0.10 |
| Marsh drier coniferous | 0.38±1.1 | 3.36±1.5 | | | >0.10 |
| Marsh wetter open | 0.82±3.0 | 0.79±2.2 | | | >0.10 |
| Water surface | 1.0±3.0 | 1.0±3.2 | | | >0.10 |
| Agriculture | 10±13 | 19±22 | -0.03±0.01 | 52 | 0.000 |
| Sea | 2.0±7.6 | 4.1±12 | -0.04±0.01 | 11 | 0.001 |
| Coniferous forest | 50±27 | 44±28 | -0.01±0.00 | 4 | 0.057 |
| Marsh drier open | 2.4±4.1 | 1.1±2.4 | 0.10±0.04 | 6 | 0.011 |

Goodness of fit: $\chi^2 = 364$, $P = 0.021$.

TABLE 8b). *Buffer 1000-m model for B. bufo*

| | Mean ± SD | | | | |
|---|---|---|---|---|---|
| Variables | Presence | Absence | Coeff (β)±SE | $\chi^2$ | *P* |
| Open land | 25±22 | 22±18 | | | >0.10 |
| Deciduous forest | 0.80±2.5 | 0.79±1.9 | | | >0.10 |
| Coniferous forest | 51±25 | 45±24 | | | >0.10 |
| Cut forest | 2.2±3.0 | 1.9±2.5 | | | >0.10 |
| Marsh limy open | 2.0±2.5 | 1.8±2.4 | | | >0.10 |
| Marsh drier open | 1.5±2.1 | 1.0±1.8 | | | >0.10 |
| Marsh drier coniferous | 0.32±0.74 | 0.33±0.88 | | | >0.10 |
| Marsh wetter open | 0.61±1.6 | 0.50±1.2 | | | >0.10 |
| Water surface | 1.3±2.8 | 1.1±3.5 | | | >0.10 |
| Agriculture | 11±11 | 20±20 | -0.04±0.01 | 59 | 0.000 |
| Sea | 4.7±11 | 6.2±15 | -0.02±0.01 | 6 | 0.017 |

Goodness of fit: $\chi^2 = 371$, $P = 0.013$.

TABLE 8c). *Combined model for B. bufo, all variables that fit in the models for buffer 500 and 1000-m.*

| Variables | Coeff (β)±SE | $\chi^2$ | *P* |
|---|---|---|---|
| Coniferous forest (500) | | | >0.10 |
| Marsh drier open (500) | | | >0.10 |
| Agriculture (500) | | | >0.10 |
| Sea (1000) | | | >0.10 |
| Agriculture (1000) | -0.04±0.01 | 59 | 0.000 |
| Sea (500) | -0.04±0.01 | 9 | 0.003 |

Goodness of fit: $\chi^2 = 369$, $P = 0.017$.

*Triturus vulgaris*

The percentage proportion of agriculture was the only variable that fit ($P<0.10$), both in the buffer models of 500 and of 1000-m width (TABLE 9a and 9b). Like for the other two amphibians, agriculture was negatively associated. The goodness of fit was $P = 0.003$ for the buffer model of 500-m, and $P = 0.002$ for the buffer model of 1000-m width.

In the combined model of the two significant variables, only the proportion of agriculture in the buffer of 500-m width was left (goodness of fit was $P = 0.005$; TABLE 9c).

TABLE 9. Results of stepwise logistic regression: buffer analyses for the presence of *T. vulgaris*. The mean value and standard deviation is given for the percentage proportion of the GIS variables in buffers around water objects with presence and absence of *T. vulgaris* respectively. The "coefficient" (β-value), probability (*P*-value) and chi-square ($\chi^2$-value) is given for all variables that fitted the model ($P < 0.10$). The "coefficient" indicates if the correlation is positive or negative, the *P*-values give the significance level and the $\chi^2$-values the contribution that each of the variables give to the goodness of fit value for the whole model.

TABLE 9a). *Buffer 500-m model for T. vulgaris*

| | Mean ± SD | | | | |
|---|---|---|---|---|---|
| Variables | Presence | Absence | Coeff (β)±SE | $\chi^2$ | *P* |
| Open land | 26±25 | 25±23 | | | >0.10 |
| Deciduous forest | 0.76±3.2 | 0.71±2.5 | | | >0.10 |
| Coniferous forest | 51±28 | 44±27 | | | >0.10 |
| Cut forest | 2.0±3.6 | 1.8±3.2 | | | >0.10 |
| Marsh limy open | 2.5±4.6 | 1.8±2.8 | | | >0.10 |
| Marsh drier open | 0.85±2.3 | 0.78±2.6 | | | >0.10 |
| Marsh drier coniferous | 0.34±1.1 | 0.38±1.5 | | | >0.10 |
| Marsh wetter open | 1.4±2.4 | 1.5±3.4 | | | >0.10 |
| Water surface | 1.0±3.1 | 1.0±3.2 | | | >0.10 |
| Sea | 3.2±10 | 3.6±12 | | | >0.10 |
| Agriculture | 10±15 | 19±22 | -0.03±0.01 | 46 | 0.000 |

Goodness of fit: $\chi^2 = 386$, $P = 0.003$.

TABLE 9b). *Buffer 1000-m model for T. vulgaris*

| Variables | Mean ± SD Presence | Absence | Coeff (β)±SE | $\chi^2$ | *P* |
|---|---|---|---|---|---|
| Open land | 25±21 | 21±19 | | | >0.10 |
| Deciduous forest | 0.75±2.3 | 0.81±2.0 | | | >0.10 |
| Coniferous forest | 49±26 | 45±24 | | | >0.10 |
| Cut forest | 2.0±2.65 | 2.0±2.64 | | | >0.10 |
| Marsh limy Open | 2.0±2.6 | 1.8±2.3 | | | >0.10 |
| Marsh drier Open | 1.2±1.8 | 1.1±2.0 | | | >0.10 |
| Marsh drier coniferous | 0.31±0.78 | 0.33±0.87 | | | >0.10 |
| Marsh wetter open | 0.58±1.3 | 0.51±1.4 | | | >0.10 |
| Water surface | 1.3±2.6 | 1.1±3.5 | | | >0.10 |
| Sea | 5.9±13 | 5.6±15 | | | >0.10 |
| Agriculture | 12±14 | 20±20 | -0.03±0.01 | 45 | 0.000 |

Goodness of fit: $\chi^2 = 389$, $P = 0.002$.

TABLE 9c). Combined buffer model for T. vulgaris, all variables that fit in the models for buffer 500-m and 1000-m.

| Variables | Coeff (β)±SE | $\chi^2$ | *P* |
|---|---|---|---|
| Agriculture (Buff 1000) | | | >0.10 |
| Agriculture (Buff 500) | -0.03±0.01 | 46 | 0.000 |

Goodness of fit: $\chi^2 = 356$, $P = 0.005$.

TABLE 10. Comparison: Goodness of fit value *(P)* of the buffer analyses between the three amphibians

| Model | *R. arvalis* | *B. bufo* | *T. vulgaris* |
|---|---|---|---|
| Buffer 500-m width | 0.308 | 0.021 | 0.003 |
| Buffer 1000-m width | 0.126 | 0.013 | 0.002 |
| Buffer combination | 0.308 | 0.017 | 0.005 |

## Land use change analysis: univariate tests

There was a significant difference between the median value of the "agricultural expansion" between the censused 1 $km^2$ where *R. arvalis* was present and absent (Mann-Whitney U-test: $Z = -2.20$; $P = 0.028$). The same results were found for *B. bufo* (Mann-Whitney U-test: $Z = -2.16$; $P = 0.031$) but for *T. vulgaris* it was not significant but a trend (Mann-Whitney U-test: $Z = -1.66$; $P = 0.097$; TABLE 11). There was no difference at all in "agricultural expansion" between km squares with presence and absence of water objects (Mann-Whitney U-test: $Z = -0.097$; $P = 0.92$)

TABLE 11. Historical analysis: Mann-Whitney U-test for comparing differences in medians of the "agricultural expansions (1700 – 2000)" between censused $km^2$ with presence and absence of "*R. arvalis*", "*B. bufo*", "*T. vulgaris*", and "all water objects" respectively. The mean value and standard deviation is given for the square meter of agricultural expansion. The *Z*-value is the test value for the differences and the *P*-value indicate the significance level ($P < 0.05$ normally indicates significance and $P < 0.10$ indicates trends in univariate tests).

| Water objects with | Mean ± SD Presence | Absence | *Z* | *P* |
|---|---|---|---|---|
| *Rana arvalis* | 71 000 ± 120 000 | 187 000 ± 241 000 | -2.20 | 0.028 |
| *Bufo bufo* | 89 000 ± 135 000 | 190 000 ± 246 000 | -2.16 | 0.031 |
| *Triturus vulgaris* | 102 000 ± 145 000 | 185 000 ± 246 000 | -1.66 | 0.097 |
| All water objects | 139 000 ± 196 000 | 188 000 ± 252 000 | -0.097 | 0.92 |

# Discussion

## The influence of water object variables on the Gotlandic amphibians

*Rana arvalis*

The environmental variables examined seemed to best explain the presence of *R. arvalis*. Absence of shadowy shoreline, large area and wide distribution of submerged vegetation gave a model with goodness of fit at $P = 0.725$, which clearly show the importance of these variables. Since *R. arvalis* prefer a spawning temperature at 10 15°C (Kuzmin 1999) and the average ambient temperature on Gotland in April (spawning period) is 2.5°C, they are expected to be dependent on sun exposed water objects. The avoidance of shadowy breeding sites agree with the study from Lindköping (southeastern Sweden) and Germany (Buch 1987, Hansen 2001), and it seems to be general for *R. arvalis* populations in most of its distribution. The positive association with water object area is difficult to separate from the shadowy shoreline since objects wider than the surrounding canopy never get the whole shoreline in shadow. If the average water temperature decreases with increasing water area the association could indicate that temperatures higher than the ambient only have relevance during springtime, when the average water temperature is low. The positive association with area agree with studies from Holland (Vos and Chardon 1998). Submerged vegetation was also significant in the analysis (in agreement with Hansen 2001), it is probably a better indicator of water permanence than water depth estimated at springtime, since the water level after the snow melting fluctuate a lot. Water plants are also an important food resource for *R. arvalis* larvae (Kuzmin 1999) and provide shelter both for adults and larvae.

The model for water classification gave a negative association with cattle pond and positive with pools. The traditional Gotlandic cattle ponds (brya) are mostly small (average area 29% smaller than the total object mean) and placed in shadow (60% higher than the total object mean), the variables *R. arvalis* dislikes. The average of the submerged vegetation index was 33% higher than the total object mean. This indicates that permanence alone did not fit the criterion for a *R. arvalis* breeding site. Pools are of a natural origin and larger (average area 10% larger than the object mean). They are of a permanent character (submerged vegetation average 18% higher index than the total object mean) and have normally sun exposed shorelines (28% lower average of shadowy shoreline than the total object mean). The goodness of fit was zero for the water classification model, in contrast to 0.725 for the environmental model. This is clearly indicating that *R. arvalis* is not connected to special water types or plant communities, single environmental variables describe their breeding sites much better.

The model for flora variables was very week, the goodness of fit ended at $P = 0.003$. *Caldium mariscus*, *Carex ssp* and *Chara ssp* entered the model and these three plants were the most common in our examined objects. The low fit value possibly indicates that none of the macrophytes in the study had any causal association with *R. arvalis*. *C. mariscus* and *Chara ssp* are indicators of nutrient-poor water quality since they are at disadvantage by eutrophication (Martinsson 1997, Van den Berg et al. 1999). *C. mariscus* is a surface crossing water plant and can possible serve as shelter for the adults during the spawning period, but since the environmental parameter "surface crossing vegetation" did not fit in the environmental model, vegetation as a shelter seems to be of minor importance. My personal impression is that *R. arvalis* breeding in vegetation poor waters are less active in daytime, a possible response to a higher exposure to predators.

None of the fauna variables had a negative influence on presence of *R. arvalis*. The positively correlated variables, "*T. vulgaris*", "other fish" and "*H. sanguisuga*", are predators on eggs, larvae and when it comes to fish (pikes) even the adult frogs, and "*B. bufo*" is a potential competitor at the larval stage. The predators could however eliminate competitors to *R. arvalis*, *Daphinia ssp* is the main food source for *T. vulgaris* and *Daphnia ssp* compete with most of the anuran larvae for the same food resource. Laboratory studies of American amphibian communities have shown that anuran larvae take advantage of *Daphnia* elimination by insecticides (Boone and Semlitsch 2001). But *Daphnia* elimination by *T. vulgaris* seems unlikely. The positively associated fauna variables were probably nothing but non-causal coexistence in the same habitat.

The combined model agreed with the environmental model with the exceptions of "submerged vegetation" which was replaced by "*Chara ssp*", the other two flora variables, *Carex ssp* and *C. mariscus* also entered. Occurrence of "*Chara ssp*" seems to better explain presence of *R. arvalis* than "submerged vegetation" since the goodness of fit value increased when "*Chara ssp*" replaced "submerged vegetation" ($P = 0.884$ for the combined model; an increase with 0.159 compared with the environmental model). "*Chara ssp*" probably indicates the importance of high water quality (Van den Berg et al. 1999) in addition to permanence. The low number of permanent water objects can probably explain the absence of *R. arvalis* in map sheet 05I8I in present day. Only two objects in the map sheet contained "*Chara ssp*" and one of them was situated within short distance from the sea (which has a negative impact on the frogs: see future discussions). We lack information of how far away the closest *R. arvalis* population is situated and we have no evidence for presence, back in time. However, a qualified guess from my side would be that the only suitable water object has been too small for inhabiting a viable *R. arvalis* population when the main wetlands in the neighbourhood got destroyed by draining.

*Bufo bufo*

"Shadowy shoreline", "area", "submerged vegetation" and "floating vegetation" entered the environmental model. The goodness of fit was $P = 0.172$, which indicates that the environmental variables had the relatively greatest influence in explaining presence of *B. bufo*. Local climate (negatively indicated by "shadowy shoreline"), permanence of water (positively associated with submerged vegetation) can be explained with the same arguments as for *R. arvalis*. Surprisingly "floating vegetation" entered the model, with a negative association. Floating vegetation is dependent on nutrient diluted in water and is therefore an indicator of eutrophication (Mulligan 1969), and habitat analyses in Stockholm have found a negative association between nitrogen and presence of *B. bufo* (Sjögren-Gulve and Karlström 1997). Even laboratory experiments have shown that moderate levels of ammonium nitrate affect larvae of *B. bufo* negatively (Oldham 1996). Sensitivity to eutrophication may explain the absence of *B. bufo* in the two map-sheets 06J5A and 07J1C since they were selected because of high proportions of agricultural land (see methods).

"Cattle pond" (negative), "marsh limy open" and "twig rush mire" (both positive) entered the water classification model. The goodness of fit was $P = 0.134$, not much lower than the fit value for the environmental variables ($P = 0.172$). This together with the overall low goodness of fit levels for the models point at *B. bufo* as a generalist in breeding site selection.

"*Chara ssp*", "*C. mariscus*", "*Lemna ssp*", and "*P. australis*" were the vegetation variables finally left in to the vegetation model. The fit was $P = 0.079$ which indicate that macrophytes directly (by their physical structure) or indirectly (as indicator for certain water condition) contribute to explain the presence or absence of *B. bufo*. "*Chara ssp*" indicate the importance of permanence, "*C. mariscus*" and "*P. australis*" are important for attaching the spawn strings (personal observation.). The positive association with "*P. australis*" can possibly be explained by coexistence with *B. bufo* in wetlands where grazing ceased. "*P. australis*" is one of the species expanding in more nutrient rich wetlands when grazing ceases (Martinsson 1997) and *B. bufo* is favoured by the dense vegetation which follows ceased grazing (Beebee 1994). The negative association with *Lemna ssp* could indicate a negative influence of eutrophication (see argumentation above), however this is contradicted by the absence of other indicators of eutrophication as *"Typha ssp"* and *"S. tabernaemontani / S.lacustris"* in the vegetation model.

None of the fauna variables effected *B. bufo* negatively and the Goodness of fit was $P = 0.001$, which indicates that predation is not of importance in breeding site selection. Eggs, larvae and possibly adult *B. bufo* avoid fish predation by being toxic (Griffiths and Denton 1992, Semlitsch and Gavasso 1992). Other studies have found positive association with fish (Beebee 1985, Sjögren-Gulve and Karlström 1997) and there are indications that *B. bufo* takes advantage of fish as an eliminator of *T. cristatus* which is the main predator of the eggs and larvae of *B. bufo* (Fog et al. 1997, Nilsson 1998). *T. cristatus* is lacking on Gotland and no *positive* association with "other fish" was found, which suggest wider choice of breeding sites in the Gotlandic *B. bufo* populations.

The combined model ended up with "shadowy shore", "area", "submerged vegetation", "floating vegetation", "marsh Limy open" and "*Lemna ssp*". In other words, the environmental variables in addition to "*Lemna ssp*" and "marsh limy open". The fit value was low ($P = 0.210$) for the model, and BMDP did not reach the convergence criterion (after 100 iterations). In other words no clear patterns were found which indirectly support that *B. bufo* is a generalist species.

*Triturus vulgaris*,
"Average water depth 1: visit", "shadowy shore", "submerged vegetation" and "dried water objects", were the environmental variables that fitted in the environmental model. A goodness of fit at $P = 0.009$, indicated that the environmental variables had very little importance for explaining the presence of *T. vulgaris*. However, "Shadowy shore" suggests that water temperature also is of some importance for *T. vulgaris*, which agrees with information from Denmark (Fog et al. 1997). The negative association with average water depth and the positive association with submerged vegetation probably indicate preference for shallow fish free water objects of permanent character.

Pools (positive) and watering pond (negative) fitted the water classification model. The goodness of fit was $P = 0.314$, indicating that these two water classes are of main importance in explaining the presence of *T. vulgaris*. The farmers often put fish in their watering ponds and pools are often too shallow and small for other fish species than sticklebacks.

In the vegetation model, "*Chara ssp*", "*Caldium mariscus*" and "*Carex ssp*" had a positive association with *T. vulgaris*. Water plants probably have a general positive effect as shelter and submerged vegetation as *Chara ssp* can also serve as deposition sites for the eggs (Fog et al. 1997). These plants are also the most common in the pools. Goodness of fit ended up with $P = 0.002$ which suggest low importance of vegetation for *T. vulgaris*.

"*Bufo bufo*", "*Rana arvalis*", "*Dytisculus marginalis*" and "*Haemopsis sanguisuga*" were positively associated with "*T. vulgaris*" and "other fish" was negative. The Goodness of fit ended at $P = 0.036$ which indicates that the fauna variables are more important in explaining presence than the plants and the environmental variables. A breeding site for other amphibians and aquatic invertebrates is a likely breeding site for *T. vulgaris* if it lacks fish with exception of sticklebacks. Fish predators are known to have a negative impact on many amphibians (Lardner and Sindenmark 1996) and newts are particularly vulnerable since their breeding period is long and the adults swim around in deeper water layers which increase the risk of confrontation. However, other studies found *T. vulgaris* less effected by fish than other newt species (Beebee 1981, Dolmen 1982, Marnell 1998).

Both water classification variables, all vegetation variables except *C. mariscus*, and the fauna variable (other fish) entered the combine model. The goodness of fit was $P = 0.059$, much lower than for the water classification model ($P = 0.314$). This suggests that the environmental variables may not describe the factors that mainly effect *T. vulgaris*. We may have missed some physical or chemical variables of importance. Studies from Ireland and Britain have found the amount of dead wood around the water object to be an important determinant of presence of *T. vulgaris* (Beebee 1985, Marnell 1998). The "amount of dead woods" around the water objects was a parameter we did not measure since all the information of the surroundings came from the GIS variables. If one assume that the amount of dead wood is negatively correlated with agricultural land, pools (mainly situated in the forest) probably covary positively and watering ponds (mainly situated in agriculture land) negatively with the amount of dead wood. The strength of the water classification model and the weakness of the environmental model could then partly be explained by this.

*Comparison of the breeding site ecology between the three Gotlandic amphibians*
Comparisons between the breeding site ecology of three amphibians point out several differences. *R. arvalis* is a specialist in comparison with *B. bufo* and *T. vulgaris* that are generalists. This is indicated by the difference in the strength of the fit value between the environmental models. The combined model improved the goodness of fit value for *R. arvalis* and *B. bufo*, but not for *T. vulgaris*, in which the water classification model was *five* times stronger than the combined model. Water classification variables entered the combined models both for *B. bufo* and *T. vulgaris*, and the convergence criterion was not reached for any of the two, probably because a lot of variables had a week influence on occupancy. This shows that *B. bufo* and *T. vulgaris* are more randomly distributed among the censused water objects - a distribution pattern expected for generalists.

## The influence of landscape variables on the Gotlandic amphibians

*Rana arvalis*
The proportion of agricultural land, sea and cut forest had a negative influence on *R. arvalis* both at a 500 and 1000-m width buffer around the water objects. Agricultural land and cut forest area are dry habitats and probably unfavourable foraging sites for *R. arvalis*, and can also have negative effects on the water quality of the water objects (Biggar and Corey 1969, Cooper 1969). It seems like *R. arvalis* occurs in agricultural areas in the main parts of the Swedish distribution, (see introduction). One explanation could be a difference in adaptation abilities to the modern farmland. The low genetic variation in combination with local adaptation to nutrient poor wetlands (see introduction) could have made the Gotlandic *R. arvalis* less resistant to the agricultural expansion than the mainland population. Salinity effects *R. arvalis* negatively (Lardner 2000), and even larger distances from the sea probably

increase the salinity of the water objects in flat open landscape. However, it should be taken into account that the highest proportion of water objects that was close to the sea was found in the cadastre map sheet 05I8I where *R. arvalis* was absent (see fig 1). The lack of *R. arvalis* in the area was probably not caused by the nearness to the sea but to lack of permanent water objects, as discussed previously. The proportion of deciduous forest was positively associated in the 500-m width buffer analysis and deciduous forest is known to have a high diversity of invertebrates (Ehnström and Waldén 1986). This is contradicted by studies of micro habitat selection from Revinge (south west Scania) that found *R. arvalis* preferring meadow and avoiding deciduous forest (Loman 1978). But deciduous forest as a GIS parameter probably includes even other microhabitats, like meadows and pastures. The data from this study suggest that *R. arvalis* is not dependent on deciduous forest for persist in an area. The map sheet that had the highest number of *R. arvalis* (06J3E; 1406 females), had only 0.9% deciduous forest in the censused buffer area and map sheet number two (07J6J; 814 females) did not have any deciduous forest at all. The highest proportion of deciduous forest had the two map sheets with the highest proportion of agricultural lands (07J1C, 28% and 06J5A, 38%). The *R. arvalis* breeding sites with deciduous forests in the neighbourhood were mostly situated in the agricultural areas. The average proportion of agricultural land in those buffers (500-m width) were more than twice (19%) the total mean proportion (8%). This suggests that deciduous forest is an important refuge area for *R. arvalis* populations in agricultural areas. Even "marsh wetter open" was positively associated with *R. arvalis* in the 500-m buffer, the main reason is probably that the densest spawning sites got that classification in the GIS system. "Marsh wetter open" contained more than six times higher average number of spawn clumps than the other marsh types, so the correlation is probably caused by a positive association with high quality breeding sites. Marshlands are also important foraging habitats for *R. arvalis* (Arnold and Burton 1977, Cedhagen and Nilson 1991, Fog et al. 1997). Studies from Uppland found migration in a direction towards marshland after the breeding season (Sjögren-Gulve 1998).

The negatively associated variables from the buffer of 500-m also fitted in the model for the buffers of 1000-m. Inhospitable habitats like agricultural land and cut forests probably have a negative influence even on a larger scale. That none of the positive variables fitted in the model for 1000-m buffers, suggests that the area within 500 meters around the spawning site is the most important foraging habitat. The model of buffer 500-m probably describes the terrestrial part of the habitat patch and the model of buffer 1000-m the matrix, which agrees with studies from Germany (Hartung 1991). The main negative influence of inhospitable habitats at the larger scale could therefore be the increase of genetic isolation. This is supported by studies from Holland finding *R. arvalis* even more sensitive to fragmentation than other anurans (Vos and Chardon 1998).

The combined model gave exactly the same results as the 500-m model, which again points out that the most important habitat structure for the adults is within 500-m from the spawning site. Also the difference in goodness of fit for the two models $P = 0.308$ for buffer 500-m and $P = 0.126$ for buffer 1000-m, confirm the major importance of the close habitat.

*Bufo bufo*

For *B. bufo* the buffer models gave no clear picture. The low goodness of fit value at 0.021 for the buffer 500-m model, 0.013 for the buffer 1000-m and 0.017 for the combined model indicate the relatively low importance of the significant variables. *B. bufo* is a habitat generalist, which agrees with my personal impression, and the literature (see introduction). Vicinity to the sea was negatively correlated with occurrence of *B. bufo*. This species can however breed in brackish water and spawning in salinity of 7‰ have been stated (Fog et al. 1997). Some of the spawning sites in this study were shallow bays with sea connections. Maybe the windy weather close to the sea has a negative impact on the local climate, resulting in the negative correlation seen. The proportion of agricultural land was also negatively associated with *B. bufo* occurence, which is in agreement with studies from Britain (Beebee 1977). Adults can however be found in the middle of arable fields (personal observation), and they are known to persist in drier habitats quite well. The modern farming methods could be a disadvantage, and agriculture deteriorates the water quality of the breeding site. Water objects close to the sea or in agricultural land also tend to be unstable and the negative association with the two variables could just be reflecting a higher proportion of water objects too "young" to be colonised. *B. bufo* is known to be a slow coloniser (Fog et al. 1997). The negative association with coniferous forest could just be the result of a large number of shadowy water objects which *B. bufo* dislikes. *B. bufo* can be found in the middle of a forest as well (personal observation) and it is one of the few amphibians in Denmark occurring in spruce cultures (Fog et al 1997). The only positive association was "marsh drier open", the most common marsh type in the buffer analyses. The density of invertebrates is probably high in marshes and therefore they are probably important foraging habitat for *B. bufo*.

*Triturus vulgaris*

Agriculture was the only GIS variable that entered the models for *T. vulgaris* (both in the 500-m and 1000-m width). The goodness of fit was $P = 0.003$ for the 500-m width model and $P = 0.002$ for 1000-m width model. In the combined model the agriculture in 500-m width was left and the goodness of fit increased to $P = 0.005$. The low goodness of fit value probably indicates that the GIS data describe the habitats on a too rough scale, much rougher than would be necessary if the habitat of *T. vulgaris* should be described with satisfaction (as discussed previously). However, the negative impact of agriculture is clear and likely (as discussed for the other amphibians). The "stronger" goodness of fit value for the 500-m buffer indicates that the negative impact of agriculture is stronger closer to the breeding site. Studies have shown that the main foraging area for *T. vulgaris* is within a short distance from the breeding site (Bell 1977, Griffiths 1984). Sea was not negatively associated with *T. vulgaris* and *T. vulgaris* is known to reproduce in brackish water with a salinity of 4 ‰ (Fog et al 1997).

*Comparison of the landscape ecology between the three amphibians*

The tendency of strength in goodness of fit is the same for the GIS models as for the field models. *R. arvalis* got the strongest combined model, *T. vulgaris* the weakest. This data further attest that *T. vulgaris* is the most generalist species in habitat choice, followed by *B. bufo*, and that *R. arvalis* have habitat requirements specified enough to be described quite well by the variables from the Swedish cadastre map system. For all species the buffer variables within 500-m of width seems to have the greatest influence. Amphibians in general have a low dispersal ability and therefore depend on the habitat close to the breeding site.

## The influence of land use changes on the Gotlandic amphibians

During the last 300 years, the agricultural land has increased less in plots (km$^2$) where *R. arvalis* and *B. bufo* are now present ($P = 0.028$ and $P = 0.031$ respectively), though not significantly so in plots where *T. vulgaris* is found ($P = 0.097$). The non-significant difference in "agricultural expansion" between km squares with presence or absence of water objects ($P = 0.92$), suggests that the significant results for the toads and the frogs were not caused by lack of censused water objects in squares where the agricultural land has increased. The changes in land use have effected the Gotlandic amphibians negatively, and *R. arvalis* and *B. bufo* have been effected most. Hence the results indicate that these species were more wide spread before the large-scale cultivation of land, which may contribute to the understanding of the general declines of amphibians in the industrial world.

## Conservation and management of the Gotlandic amphibians

None of the Gotlandic amphibians are in danger at the moment, but regionally *R. arvalis* have probably decreased during the last century, as a result of marsh land draining and agricultural expansion. Special attention should also be taken to the Gotlandic *R. arvalis* populations since they are classified as an evolutionary significant unit (Lindgren 2001). The cultivation of new land does not increase any more, but what probably threatens the remaining *R. arvalis* populations on Gotland is modern silviculture, with large drained clear-cut areas (as indicated in this study), and other land exploitation such as road constructions and summer cottages, which increases the fragmentation. On basis of the results of this investigation the general advice to the local authorities would be to prevent land exploitations (road constructions etc), larger clear cutting and draining in an area of at least 500-m, both from known *R. arvalis* localities and from "potential localities". As "potential localities" all marshes defined as wetter open or limy open (in the cadastre map GIS system) should be counted, until the amphibian fauna has been examined.

During the last years it has become popular to dig up marshes in purpose of creating a permanent pond attractive for hunting game, mainly birds (Martinsson 1997). It is important not to permit these transformations unconditional of known and potential *R. arvalis* localities. The following demands are recommended in purpose to minimise the negative impact on the amphibians: a wide zone of sun exposed shoreline of water vegetation should be saved. It is also important not to connect the marsh with creeks or ditches as surface water will then contribute to eutrophication and fish will be given an opportunity to establish in the water object. Even the eutrophication that results from introduced ducks or feeding of wild ducks is devastating for the amphibian populations and should be avoided in known and potential breeding sites (Fog 1993).

## Conclusions

*R. arvalis* seems to be quite specialised in habitat requirements. A clear preference for sun exposed large and permanent water objects with vegetation of *Carex ssp*, *C. mariscus* and *Chara ssp* where found and explained 88.4% of the observations. The significant variables from the Geographical Information System (GIS), indicate that modern farming and clear cutting had a negative impact of the frogs. Deciduous forest seems to be important in the agricultural areas. The proportion of the significant GIS variables in buffers of 500 meter around the breeding sites explained 30.8% of the observations of *R. arvalis*. This is surprising since *R. arvalis* populations on the Swedish mainland seem to be generalists and common in farmlands. In agreement with other studies *T. vulgaris* and *B. bufo* seems to be habitat generalists even on Gotland, indicated by low agreement between the models and the observations. Negative association with watering ponds and positive association with pools explained 31.4% of the observations of *T. vulgaris*. Sun exposed shore, area, permanence (indicated as submerged vegetation) and avoidance of eutrophication (indicated as floating vegetation) explained 21% of the *B. bufo* observations. The GIS variables did not explain occurrence of the two species with any confidence. The expansion of agricultural land during the last 300 years has significantly effect the distribution of *R. arvalis* and *B. bufo*, and could probably contribute to explaining the declines of amphibian populations in the industrial world.


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# APPENDIX 1

*Descriptive statistics of the water object variables*

| variables | Minimum | Maximum | Mean±SD |
|---|---|---|---|
| Log Area ($m^2$) | 2.92 | 14.09 | 7.6±2 |
| Submerge veg (category) | 0 | 4 | 0.90±1.1 |
| Floating veg (%) | 0 | 100 | 1.7±5.9 |
| Surface crossing veg (%) | 0 | 100 | 22.±29 |
| Average w depth 1: visit (m) | 0 | 2 | 0.40±0.32 |
| Maximum w depth 1: visit (m) | 0.10 | 3 | 0.72±0.46 |
| W depth change (m) | -0.50 | 0 | -0.03±0.08 |
| Average w depth 2: visit (m) | 0 | 2 | 0.37±0.34 |
| Maximum w depth 2: visit (m) | 0 | 3 | 0.69±0.48 |
| Dried w objects | 0 | 1 | 0.013±0.11 |
| Shadowy shore (%) | 0 | 100 | 23±28 |
| Shallow shore (%) | 0 | 100 | 55±41 |
| Twig rush mire (agmyr) | 0 | 1 | 0.16±0.37 |
| Temporary wetland (vät) | 0 | 1 | 0.23±0.42 |
| Watering pond | 0 | 1 | 0.095±0.29 |
| Cattle pond | 0 | 1 | 0.13±0.34 |
| Open cast | 0 | 1 | 0.12±0.32 |
| Pool | 0 | 1 | 0.36±0.48 |
| Flood | 0 | 1 | 0.18±0.38 |
| Marsh limy open | 0 | 1 | 0.20±0.40 |
| Marsh drier coniferous | 0 | 1 | 0.019±0.14 |
| Marsh drier open | 0 | 1 | 0.30±0.46 |
| Marsh wetter open | 0 | 1 | 0.082±0.28 |
| *C. mariscus* (%) | 0 | 100 | 19±30 |
| *P. australis* | 0 | 1 | 0.12±0.33 |
| *Carex ssp* | 0 | 1 | 0.43±050 |
| *S. tabernaemontani / S. lacustris* | 0 | 1 | 0.038±0.19 |
| *Lemna ssp* | 0 | 1 | 0.022±0.15 |
| *Typha ssp* | 0 | 1 | 0.14±0.35 |
| *Chara ssp* | 0 | 1 | 0.21±0.41 |
| *R. arvalis* (#) | 0 | 1073 | 14±69 |
| *Bufo bufo* (category) | 0 | 4 | 0.71±1.3 |
| *T. vulgaris* (category) | 0 | 4 | 0.43±0.73 |
| *P. pugitius / G. aculetus* (category) | 0 | 4 | 0.080±0.39 |
| Other Fish | 0 | 1 | 0.035±0.18 |
| *H. medicinalis* | 0 | 1 | 0.0095±0.097 |
| *H. sanguisuga* | 0 | 1 | 0.070±0.25 |
| *D. marginalis* | 0 | 1 | 0.0095±0.097 |

# APPENDIX 2

Occurrence of the binary variables in the censused water objects.

| Variables (0 / 1) | Absence | Presence |
|---|---|---|
| Dried w objects | 311 | 4 |
| Twig rush mire (agmyr) | 264 | 50 |
| Temporary wetland (vät) | 242 | 72 |
| Watering pond | 284 | 30 |
| Cattle pond | 272 | 42 |
| Open cast | 277 | 37 |
| Pool | 199 | 115 |
| Flood | 256 | 58 |
| Marsh limy open | 250 | 64 |
| Marsh drier coniferous | 308 | 6 |
| Marsh drier open | 219 | 95 |
| Marsh wetter open | 288 | 26 |
| *P. australis* | 277 | 38 |
| *Carex ssp* | 179 | 136 |
| *S. tabernaemontani / S. lacustris* | 303 | 12 |
| *Lemna ssp* | 308 | 7 |
| *Typha ssp* | 271 | 44 |
| *Chara ssp* | 248 | 67 |
| Other Fish | 304 | 11 |
| *H. medicinalis* | 312 | 3 |
| *H. sanguisuga* | 293 | 22 |
| *D. marginalis* | 312 | 3 |

## APPENDIX 3

*Descriptive statistic of the proportion GIS variables in Buffers around 315 monitored water objects the data was taken from the cadastre map (2001)*

*Buffers of 500-m in wide (percentage proportion)*

| Variable | Minimum | Maximum | Mean±SD |
|---|---|---|---|
| Agriculture | 0 | 82.8 | 16±20 |
| Open land | 0 | 93.8 | 25±23 |
| Deciduous forest | 0 | 25.8 | 0.70±2.7 |
| Coniferous forest | 0 | 97.8 | 46±28 |
| Cut forest | 0 | 23.13 | 1.9±3.4 |
| March limy open | 0 | 25.6 | 2.0±3.5 |
| March drier coniferous | 0 | 12.6 | 0.4±1.4 |
| March drier open | 0 | 23.9 | 1.5±3.1 |
| March wetter open | 0 | 25.0 | 0.8±2.5 |
| Water surface | 0 | 28.0 | 1.0±3.2 |
| Sea | 0 | 67.6 | 3.4±11 |

*Buffers of 1000-m in wide (percentage proportion)*

| Variables | Minimum | Maximum | Mean±SD |
|---|---|---|---|
| Agriculture | 0 | 84.8 | 17±18 |
| Open land | 0 | 72.4 | 22±20 |
| Deciduous forest | 0 | 13.4 | 0.80±2.1 |
| Coniferous forest | 0 | 95.9 | 46±25 |
| Cut forest | 0 | 15.4 | 2.0±2.6 |
| March limy open | 0 | 12.1 | 1.9±2.4 |
| March drier coniferous | 0 | 5.2 | 0.30±0.80 |
| March drier open | 0 | 12.6 | 1.2±1.90 |
| March wetter open | 0 | 10.2 | 0.50±1.40 |
| Water surface | 0 | 23.8 | 1.2±3.3 |
| Sea | 0 | 67.5 | 5.7±14 |

*Descriptive statistic of the GIS data from the monitored 1 x 1 $Km^2$ squares (unit $m^{-2}$) in the cadastre maps from 18:th and 21:th century*

| Variable | Minimum | Maximum | Mean±SD |
|---|---|---|---|
| Agriculture 1700 | 0 | 429 000 | 41 000±70 000 |
| Agriculture 2000 | 0 | 942 000 | 203 000±270 000 |
| Lake 1700 | 0 | 655 000 | 11 000±68 000 |
| Water surface 2000 | 0 | 655,000 | 11 000±69 000 |
| Meadow 1700 | 0 | 984 000 | 92 000±175 000 |
| Pasture 1700 | 0 | 743 000 | 97 000±161 000 |
| Open land 2000 | 0 | 800 000 | 134 000±173 000 |
| Mire 1700 | 0 | 982 000 | 73 000±163 000 |
| Marsh limy open 2000 | 0 | 268 000 | 12 000±29 000 |
| Marsh drier coniferous 2000 | 0 | 138 000 | 5 000±16 000 |
| Marsh drier open 2000 | 0 | 302 000 | 15 000±33 000 |
| Marsh wetter open 2000 | 0 | 279 000 | 5 000±24 000 |
| Conifourus forest 2000 | 0 | 990 000 | 504 000±314 000 |
| Cut forest 2000 | 0 | 361 000 | 27 000±45 000 |
| Deciduous forest 2000 | 0 | 271 000 | 9 000±36 000 |

# Vad kännetecknar de miljöer som det gotländska groddjuren är beroende av

**Mattias Sterner**

Groddjur är beroende både av en vattenmiljö och en landmiljö för att kunna fortleva, det gör dem extra känsliga för miljöförändringar. Det finns också indikationer på att groddjuren minskat i en oroande takt runt om i världen. Eftersom kunskapen är bristfällig om vilka miljöer som är viktiga för groddjuren, bestämde jag mig för att ta reda på vilka faktorer som skiljer ut vatten där groddjur reproducerar sig. Jag ville också undersöka hur groddjuren påverkats av det moderna jord och skogsbrukslandskapet.
Studien genomfördes på Gotland där tre groddjur förekommer i dag. Det är mindre vattensalamander (Triturus vulgaris), vanlig padda (Bufo bufo) och åkergroda (Rana arvalis). Jag jämförde både vattenvariabler, och landskapsvariabler (från fastighetskartan) runt vattnen, mellan de lokaler som hade och inte hade förekomst av det tre groddjuren. Dessutom jämförde jag ökningen av den uppodlade arealen, det senaste 300 åren mellan kvadratkilometerutor med respektive utan förekomst av groddjur.
Stora och permanenta vatten med hög andel solexponerad strand och typisk vattenvegetation för näringsfattigt vatten var mest populära för åkergrodan och den vanliga paddan. Gölar utan fisk var mest betydelsefulla för den mindre vattensalamandern. Åkergroda verkar vara mer kräsen i sitt val av lekvatten än de andra två arterna, dessutom verkar landskapet ha stor betydelse för var den förekommer. Med lövskog och våtare sumpmarker inom 500 m från lekvattnet trivs åkergrodan. Det viktigaste verkar dock vara att det inte finns för mycket åkermark och kalhyggen, inom den närmaste kilometern från dess lekvatten. För det andra två arterna verkar inte det omgivande landskapet ha någon större betydelse. Den odlade arealen hade ökat betydligt mer, under det senaste 300 åren, i de kvadratkilometer rutor där det inte förekom vanlig padda eller åkergroda.
Att lekvattnets lokalklimat (solexponeringen) är speciellt viktig för åkergrodan kan man förvänta sig eftersom de vill ha en ganska hög temperatur för att lägga rom. Stora och permanenta vatten har fördelen att de inte torkar ut innan grodynglen hinner genomgå förvandlingen till grodor. Åkergrodan och den vanliga paddan verkar också trivas i de vatten där det finns växter som är typiska för en näringsfattig miljö, vilket kan tyda på att dessa två arter är känsliga för övergödning. Rovfisk är nog ett större problem för den mindre vattensalamandern än för det andra två groddjuren efter som den rör sig i vattnets djupare delar och därför är lättare att upptäcka för fiskar. Den mindre vattensalamandern tycks annars föredra gölar. Detta kan ha ett samband med att dessa ofta är belägna i skogsmark, där det finns multnande stubbar och andra för vattensalamandrar trivsamma landmiljöer (även vattensalamandrar lämnar vattnet och beger sig upp på land när leken avslutats). Lövskog och våtare sankmark är säkert viktiga födosöksmiljöer för åkergrodan, till skillnad från åkermark och kalhyggen som är torra och ogästvänliga för grodor. Det sist nämnda miljöerna kan dessutom öka lekvattnens isolering vilket kan leda till problem med inavel. Att vanlig padda och åkergroda verkar ha minskat under nittonhundratalet kan kanske delvis förklaras med den kraftiga uppodling av våtmarker som skett de senaste seklerna. Därför hoppas jag att denna undersökning ska vara till hjälp i det framtida bevarande arbetet av Gotlands groddjur. Speciellt viktigt är det att ta hänsyn till den gotländska åkergrodan, efter som den anses vara en så kallad signifikant evolutionär enhet, vilket innebär att den kommer att kunna utvecklas till en egen art i framtiden.

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