# REPTILE ABUNDANCE IN TEMPERATE-ZONE EUROPE: EFFECT OF REGIONAL CLIMATE AND HABITAT FACTORS IN LATVIA

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The role of large-scale factors in influencing reptile abundances in temperate-zone lowland Europe is relatively obscure. Data on relative abundances of reptiles were collected in various regions of Latvia. Multiple regression analysis was used to determine the relationship between reptile abundance and climate and habitat predictors. For lizards, habitat was a more important regional-scale factor than climate, although warmth of summer was important in *Lacerta agilis*. For snakes, however, climate was a highly significant factor. *Natrix natrix* in Latvia is common only in areas with mild winter climate at elevations below 50 m a.s.l., while *Vipera berus* is frequent in upland areas with relatively harsh winters. Potentially, the latter species could be negatively affected by global warming.

**Keywords:** reptiles, abundance, climate, habitats, temperate-zone Europe, Latvia.

## 1. INTRODUCTION

Numerous factors can affect the distribution and abundance of reptiles, including climate, topography, habitat composition, and intensity of various anthropogenic impacts. Many studies have been done on habitats of European reptiles (e.g., House and Spellerberg, 1983; Stumpel, 1985; Berglind, 2000), but the role of climate factors in temperate-zone Europe has been largely overlooked. The influence of climatic factors is perhaps best tested at species' distribution limits, either latitudal or altitudinal (Gaston, 2003). The significance of climatic factors in influencing the occurrence of reptiles in lowland temperate-zone Europe, where many species have large ranges, remains obscure. Reptiles are ectotherms, and their ecology and habitat preferences can be strongly determined by regional climate (Jablokov, 1976; Pikulik et al., 1988). Thus, knowledge of preferred climatic conditions also is important for species conservation, particularly establishment of protected areas. Latvia is a relatively small lowland country. Nevertheless, it has a marked climate transition from relatively maritime in the west to more continental in the east (Kavacs, 1995), making it very suitable for climate-related research.

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Recent practice in climate and landscape studies of reptiles is to use GIS with base layers of data on climate, land cover, topography, and presence-absence of species (Guisan and Hofer, 2003; Raxworthy et al., 2003). In contrast, the present study is based on extensive fieldwork and uses multiple regression to predict relative species abundance from climatic and habitat variables. Such approach would be more sensitive than the usage of only presence-absence data.

This paper presents some of the results of a wider survey conducted to clarify the factors determining distribution and abundance of reptiles in Latvia. Here, I consider only the influence of large-scale climatic and habitat factors. Habitats here are regarded in very broad sense, e.g., forest habitats include not only more or less closed forest, but various ecotopes (clearings, cuttings, etc.) as well. Survey transects were located mostly along linear structures such as roadsides, verges, and paths, although intact habitats were surveyed as well. The average human population density on each study plot also was selected for analysis, as an indicator of the impact of potential settlement and direct human presence (killing of snakes, etc.). Information from topographic maps about altitude and the surrounding landscape (forest, open landscape, mire, urban area) also was used.

Because reptile abundance also is affected by local factors, I included variables characterizing the various transects (e.g., proportion of different verge types) in my

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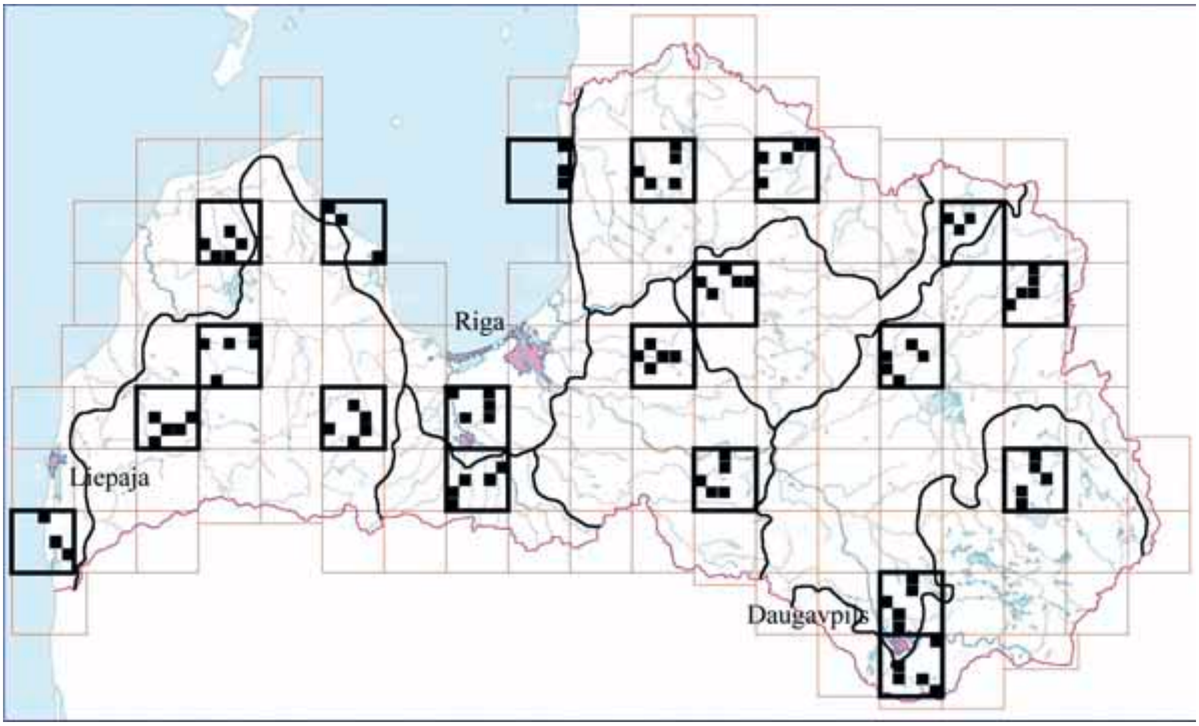


**Fig. 1.** Location of sampled 25 × 25 km plots and sampled 5 × 5 km squares in geo-botanical regions of Latvia.

original analyses. However, as none of these factors were significant, I left them out of the analyses printed here.

## 2. METHODS

### 2.1. Study Area

Latvia is located on the Mid-Eastern coast of the Baltic Sea, from 55 – 58° N 21 – 28° E. About 60% of the territory lies below 100 m a.s.l., and only 3% above 200 m (Kavacs, 1997). Average temperatures range from –3 to –7°C in January, and 16.5 – 17°C in July, average annual precipitation is 550 – 850 mm, sum of active temperatures 1770 – 2155°C (Kavacs, 1995). The entire country is in the sub-boreal forest zone and about 45% of it is covered by forest, dominated by Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* L.), and birch (*Betula pendula* Roth, *B. pubescens* Ehrh.) (Broks, 2003); about 5% of the country consists of mires, mostly of the raised-bog type (Kavacs, 1997). Large-scale anthropogenic impact in Latvia is moderate: population density Latvia is low, less than 15 inhabitants per $km^2$ (Overview of the Latvian indicators of sustainable development, 2003), and management of agricultural lands is mainly low intensity (Bergkaute et al., 1999).

### 2.2. Sampling

Sampled sites were selected at random from stratified plots. Twenty 25 × 25 km plots from the Baltic Coordinate System were chosen, 1 – 5 in each geo-botanical region of Latvia. Geo-botanical zoning was employed because it encompasses many factors, such as soil, geology, geomorphology, and climate, not just vegetation characteristics (Kavacs, 1995). Three to five 5 × 5 km squares were randomly selected from each 25 × 25 km plot (total of 92). The number of selected squares in each region was roughly correlated with its area (Fig. 1). Reptiles were counted on transects that crossed 5 km squares in random direction through their central parts.

Censuses were carried out mostly along verges of minor roads and paths to facilitate walking and observation of reptiles. Censuses were carried out once on each transect, in the field seasons (May–September) of 1999 – 2003. As the activity and observed frequency of reptiles vary during a season (e.g., Jablokov, 1976; Kosov, 1983; Glandt, 1995), transects in the same 25 km plot were surveyed in different months to reduce the impact of this factor on abundance estimates. Similarly, transects within plots also were surveyed in different years to account for inter-year density fluctuations. Censuses were carried out over 5 – 9 h in dry and warm (19 – 25°C) weather. Surveys were interrupted at midday of hot days and during unfavorable weather (falling temperature, showers). Because all reptile species had low overall densities, differences in transect widths related to variation in habitat-specific ground cover (and hence observability of reptiles) were ignored. The total length of transects was 689.3 km (average 7.5 km per 5 × 5 km square).

### 2.3. Topographic Data

Altitudes and total coverage of landscapes (forest, open landscapes, mires, urban areas) within a circle of 2.5 km radius around each reptile observation were acquired from topographic maps (1996 – 1997) with scale 1:50,000. Degree of landscape fragmentation (average size of given landscape fragment) was also determined, but not used in analyses, because it had positive correlation with coverage in all cases ($p < 0.05$). For each species, mean values of all observations in the same 5 × 5 km square were used. A random sample was taken of altitudes in the center of, and from landscapes within, a 2.5 km radius circle around the center of each sampled 5 × 5 km square. In total, data were obtained for 12 squares occupied by *Lacerta agilis*, 89 by *Zootoca vivipara*, 32 by *Anguis fragilis*, 15 by *Natrix natrix*, 18 by *Vipera berus*, and 92 random squares.

Differences between the random sample and reptile sites were evaluated by the Mann–Whitney (Wilcoxon) *W*-tests. In the case of significant altitude preferences for a species, only landscapes from the appropriate altitude range were compared.

### 2.4. Multiple Regression Analysis

Stepwise multiple regression (with *F* — to enter and remove variables at 4.0) was performed to assess relationships between relative abundance of reptiles, and the following predictors: climate factors, average human population density (from Turlajs, 1998), and proportion of different habitats along transects.

The distributions of four species (*Lacerta agilis*, *Anguis fragilis*, *Natrix natrix*, *Vipera berus*) were uneven, and their average densities on transects were very low (0.03 – 0.07 records per km). Therefore, relative abundance data for these species were expressed as the proportion of occupied 5 × 5 km squares in each 25 × 25 km plot. By contrast, *Zootoca vivipara* was observed in all 25 × 25 km plots (average abundance, 0.51 records per km); variation in density between years also was not statistically significant for this species (ANOVA, $p > 0.1$). Thus, for *Z. vivipara*, relative density data in plots were used in analyses (records of juveniles were omitted to reduce seasonal differences).

Climate variables were acquired from published maps (Temnikova, 1958; Kavacs, 1998). Principal Component Analysis (PCA), with varimax rotation, was used for climate data reduction and to better capture environmental gradients (Brūmelis et al., 2000). The original variables were replaced by the smallest number of uncorrelated principal components (eigenvalue > 1.0) that encompassed 80% or more of total variability. These principal components were then used as predictors in subsequent multiple regression analysis.

Data on habitats along transects were acquired from field descriptions. They were classified as follow:

- deciduous trees (mostly *Betula* spp., *Alnus incana* L., *Populus tremula* L. dominated) stands: (a) dry and (b) wet;
- coniferous trees (*Pinus sylvestris* L., *Picea abiea* L.) stands: (a) dry and (b) wet;
- mires of various types (mostly bogs), including drained ones;
- forest edges with open habitats, of various stands;
- meadows and fallow lands, with or without sparse low shrub cover;
- various agricultural landscapes (crops, gardens, etc.).

Habitat data were square-root ($x + 0.5$) transformed (successful normalization in all but mire and agrolandscape types). Multicollinearity within the habitat data was low (one of 27 correlations at $p < 0.05$, and two more at $p < 0.1$). All statistics were performed with STATGRAPHICS Plus® software.

## 3. RESULTS

### 3.1. Species Encountered

Five of the seven native species of reptiles were observed on transects in this survey. *Lacerta agilis* was found on 13% of visited 5 × 5 km squares, *N. natrix* on 16%, *V. berus* on 20%, *A. fragilis* on 35%, and *Z. vivipara* on 96%. Two species were absent: the Pond Turtle *Emys orbicularis* is very rare (Ingelog et al., 1993), aquatic (Arnold, 2002), and possibly introduced (Čeirāns, unpublished data); the Smooth Snake *Coronella austriaca* also is very rare and confined to the narrow coastal zone of western Latvia (Čeirāns, 2000).

### 3.2. Analyses from Topographic Maps

In *N. natrix*, observed altitudes differed significantly from the random sample ($p = 0.00002$, Fig. 2). This spe-

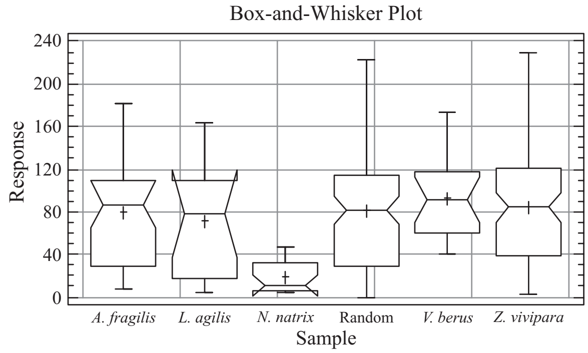


**Fig. 2.** Altitudes of reptile observations and random sample (mean values marked with cross).

cies was found only at elevations below 50 m a.s.l. Notable also was the absence of *V. berus* below 40 m a.s.l., although the elevation range of this species was not significantly different from that of the random sample.

Two species had statistically significant landscape preferences. The landscapes inhabited by *A. fragilis* had higher forest coverage (range, %; mean ± S.E.; median: 36 – 95; 69 ± 3; 70) and lower open landscape coverage (4 – 64; 26 ± 3; 26), than random sites [(1 – 97; 54 ± 2; 57) and (0 – 96; 41 ± 2; 39), respectively]. These differences were significant at $p < 0.01$. *Vipera berus* inhabited areas with higher coverage of mires (0 – 40; 8 ± 3; 2) than sites in the random sample (0 – 69; 4 ± 1; 0.05). The difference was significant at $p = 0.03$. There were no differences in urban coverage between landscapes inhabited by reptiles and a random sample ($p > 0.1$).

### 3.3. PCA on Climate Variables

PCA grouped climate variables in three components that accounted for 83% of the total variance (Table 1). PCA 1 accounted for 47% of the variance and had positive loadings from variables characterizing mild and short winters. PCA 2 (25% of the variance) had positive loadings from variables characterizing high rates of precipitation and PCA 3 (12%) from variables characterizing long and hot summers.

### 3.4. Predictors of Abundance

In the multiple regression analysis, reptile abundance was predicted only by climate and habitat factors. No relationships were found between reptile abundance and human population density. The latter varied between 6.0 and 23.5 (12.5 ± 1.3) persons per km$^2$.

The abundance of *L. agilis* was predicted by a combination of two factors: climate (hot summers, PCA 3), and the proportion of dry coniferous forest, of which the more important was the habitat factor ($R^2_{adj} = 48\%$, DW = 2.20, $T_{PCA\,3} = 2.50$, $T_{DryCon} = 3.25$, $p = 0.0014$).

The abundance of *Z. vivipara* was predicted mostly by habitat type and the influence of climate was somewhat less important. This species was most abundant in wet coniferous forests with cool summers ($R^2_{adj} = 36\%$, DW = 2.46, $T_{PCA\,3} = -1.99$, $T_{WetCon} = 2.43$, $p = 0.0086$).

In three species, abundance was predicted by single factor. Abundance of *A. fragilis* was negatively related to the proportion of agricultural landscapes ($R^2_{adj} = 33\%$, $p = 0.0049$, Fig. 3). The abundance of the two snake species were both predicted by the same climate factor (PCA 1), but in opposite directions. *Natrix natrix* was more abundant in areas with relatively mild winters

**TABLE 1.** Weight of Climate Parameters in PCA After Varimax Rotation

| Parameter | Component 1 | Component 2 | Component 3 |
|---|---|---|---|
| Precipitation in warm (April – October) season | –0.50 | **0.81** | –0.07 |
| Precipitation in cold (November – March) season | 0.22 | **0.90** | –0.24 |
| Annual precipitation | –0.07 | **0.93** | –0.12 |
| Days with snow cover | **–0.96** | 0.13 | 0.05 |
| Percentage of winters with unsteady snow cover | **0.90** | –0.12 | –0.13 |
| Air temperature in January | **0.93** | –0.13 | 0.27 |
| Air temperature in July | –0.10 | –0.47 | **0.72** |
| Frost-free period on ground | **0.65** | –0.06 | 0.51 |
| Frost-free period on grass | **0.94** | 0.07 | –0.12 |
| Frost-free period in air | **0.75** | –0.08 | 0.23 |
| Period with mean temperature > 10°C | –0.18 | –0.01 | **0.84** |
| Period with mean temperature > 5°C | **0.86** | 0.17 | 0.31 |
| Sum of active temperatures | 0.37 | –0.24 | **0.84** |
| Annual number of cloudy days | **–0.82** | 0.31 | –0.12 |

**Note.** Boldface, parameters with weight > 0.55 used in data reduction.

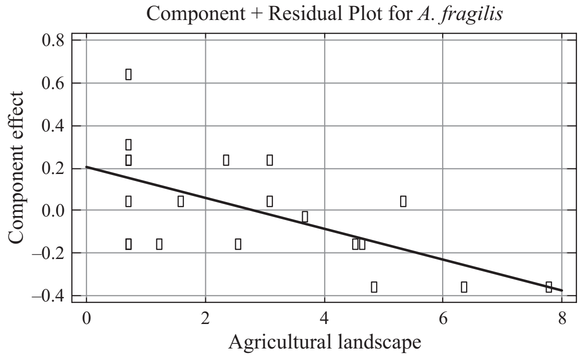


**Fig. 3.** Relationship between the abundance of *A. fragilis* and the proportion of agricultural landscapes ($p = 0.0049$).

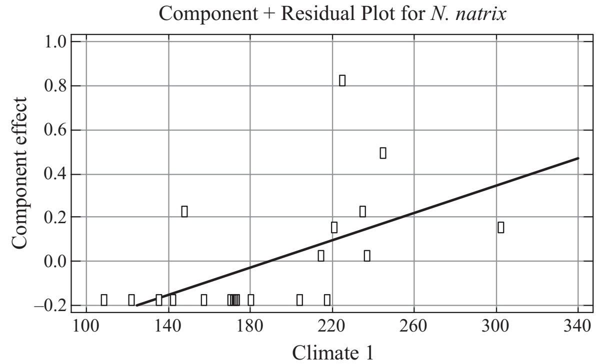


**Fig. 4.** Relationship between the abundance of *N. natrix* and PCA 1 (mild winters; $p = 0.013$).

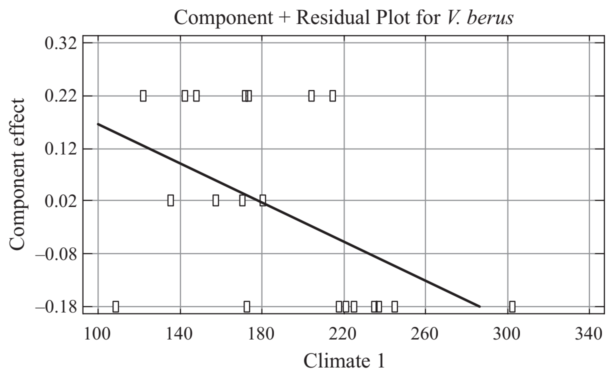


**Fig. 5.** Relationship between the abundance of *V. berus* and PCA 1 (mild winters; $p = 0.028$).

($R^2_{adj} = 26\%$, $p = 0.013$, Fig. 4) and *V. berus* in areas with relatively cold winters ($R^2_{adj} = 20\%$, $p = 0.028$, Fig. 5).

Because both snake species had restricted elevational distributions, the pronounced effect of climate on their abundance might simply reflect altitude (correlation between winter weather and altitude across plots, $r = -0.84$, $p < 0.0001$) and thereby obscure effects of other factors. Therefore, I reduced the effect of climate by excluding plots outside the observed elevation range of the species; only plots from elevations above 40 m a.s.l. for *V. berus* ($n = 14$), and from elevations below 50 m a. s. l for *N. natrix* ($n = 8$) were selected for further analysis. At this scale, abundances of both species were positively related to various wet habitats: *N. natrix* — all wet forests and mires ($R^2_{adj} = 78\%$, DW = 2.09, $T_{Mire} = 2.65$, $T_{WetDec} = 2.97$, $T_{WetCon} = 3.84$, $p = 0.029$), *V. berus* — wet coniferous forests and mires ($R^2_{adj} = 41\%$, DW = 2.40, $T_{Mire} = 2.10$, $T_{WetCon} = 2.40$, $p = 0.022$).

## 4. DISCUSSION

In this study, I found significant effects of both habitat and climatic factors on abundance of reptiles in Latvia, but the particular effects varied among species. However, because given species may have different habitat and climate preferences in other climatic zone (e.g., Jablokov, 1976; Pikulik et al., 1988), my conclusions, strictly speaking, apply only to the European sub-boreal forest zone and should be extrapolated to populations elsewhere with caution.

Abundance of snakes was affected mainly by winter weather, but in opposite directions in the two species. *Natrix natrix*, which is more abundant in areas with mild winters, is restricted in elevation in Latvia to areas below the 100 m isobar (Fig. 6), with only few records at elevations about 120 m a.s.l. This species is relatively common only in areas below 50 m. By contrast, *Vipera berus* is more abundant in areas with relatively harsh winters, more characteristic of uplands, and Eastern and Northern Latvia. In this survey, *V. berus* was not found in the Coastal Lowland, in spite of known records there.

Due to given abundance pattern, the latter species may face threats from global warming. There has been a distinct climate-warming trend in Europe during the 20th century, with a mean increase in annual temperatures of about 0.8°C, but exceeding 3°C in some northern and central areas of European Russia. This warming event was exceptionally rapid during the 1980s, with increases of 0.25 – 0.5°C per decade (IPCC, 2001). The recent climate change has had important ecological consequences for various organisms and ecosystems (Walther et al., 2002). As the temperature increase has been particularly evident during the winter period (IPCC, 2001), climate warming could have a particularly adverse effect on *V. berus*. Although lack of data on numbers prevents firm conclusions about abundance trends

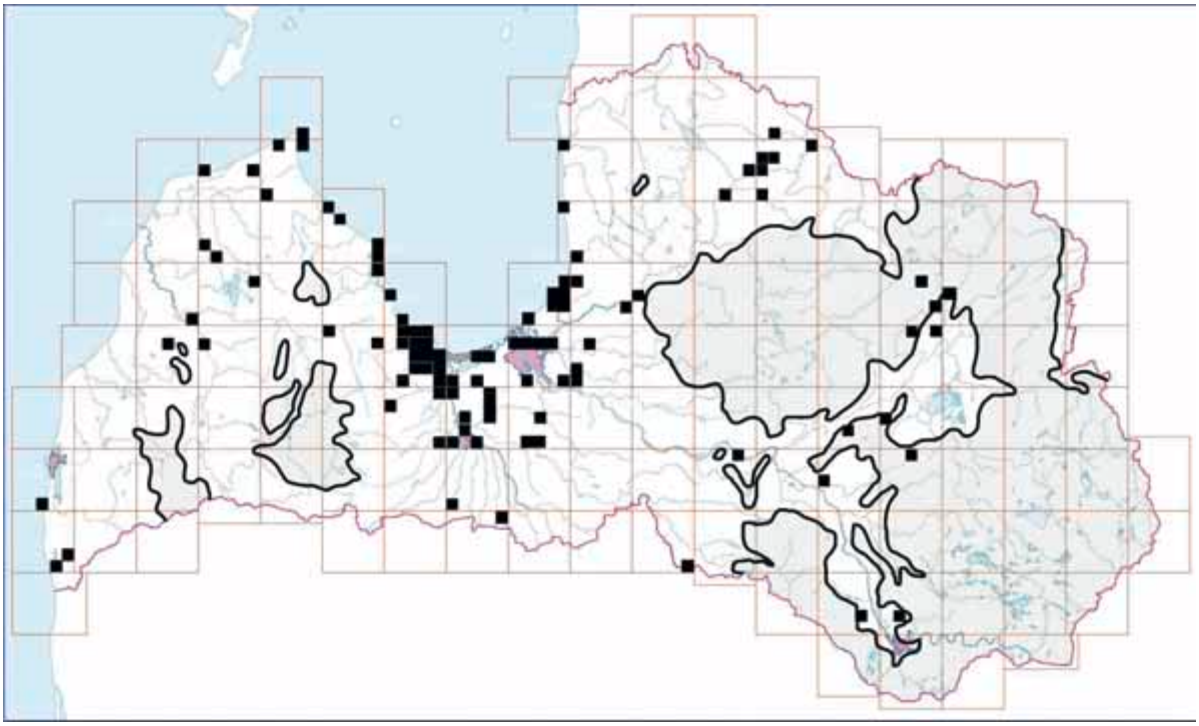

**Fig. 6.** The distribution of *Natrix natrix* in 1990 – 2004 (solid squares), and the area above 100 m isobar (pale).

in Latvia, there is indirect evidence of declines of *V. berus*, at least in some protected areas, since the 1980s (Čeirāns, 2002b). This species prefers to hibernate in collective dens on slopes with southern exposure (Viitanen, 1967; Prestt, 1971), where the snow cover is less stable. Reduced snow cover in winter could cause a drastic increase in winter mortality of snakes due to freezing (Shine and Mason, 2004). Thaws with following frosts would less likely happen in uplands with harsher climate, what possibly explains observed abundance pattern for *V. berus* in Latvia. Another contributing factor to increased winter mortality could be loss of fat reserves when hibernating temperatures are too high (Costanzo, 1989). Low fat reserves post-hibernation also could negatively affect reproductive success (Prestt, 1971). However, this factor would be less important in Latvia, because average winter temperatures there are still low.

Although habitat factors were not important influences on abundance of snakes at the regional scale, both species were more abundant in areas with higher proportions of various wet habitats. The connection of *N. natrix* with wet habitats is well known; such habitats are important for its main food resource — amphibians (Drobenkov, 1995; Gregory and Isaac, 2004). Mires and other wet habitats are regarded as typical for *V. berus* (Boshansky and Pishchelev, 1978; Phelps, 1978; Stumpel, 1992; Zuiderwijk et al., 1998), although not obligate (Belova, 1976). Both species are versatile, have large home ranges, often with different wintering, mating, and summer grounds (Viitenen, 1967; Prestt, 1971; Phelps, 1978; Madsen, 1984). Hence, local factors such as prey abundance, presence of suitable egg-laying and wintering sites, topography, etc. could be more important than broad habitat types like in the present survey.

In contrast to snakes, abundance of lizards in Latvia was affected by regional variations in both climate and habitat, especially the latter. The most important climatic factor was summer weather, which influenced abundance of lacertid species. With respect to habitat factors, abundance of the two lacertid species was positively influenced by coniferous forests and that of *A. fragilis* was negatively affected by agricultural landscapes.

Although the most significant regional factor for *L. agilis* in Latvia is presence of dry coniferous forest habitats, only parts of this broad habitat type are actually suitable. These are well-lit, open ecotopes of dry pine-dominant forests on sandy soils, and habitats created after their clearing, covered by grasses and undershrubs, interspersed with bare patches (Čeirāns, 2002b, 2004). Similar habitats on sand are typical for this species in the northern part of its range (House and Spellerberg, 1983;

Stumpel, 1988; Berglind, 2000). However, summer temperatures also are important. The highest densities of *L. agilis* were observed in South-Eastern Latvia, an area with a relatively continental climate.

*Zootoca vivipara* is very widespread and the most common reptile species in Latvia. It is found most often in areas with a high proportion of wet coniferous forest, which is verified by surveys done in forests (Čeirāns, 2004). This species also is more abundant in areas with cool summers, but this factor is less important than habitat.

Habitat composition is a significant determinant of the abundance of *A. fragilis* in Latvia. This species is frequent in forested areas and rare in open ones, especially agricultural. The preference for more-or-less forested habitats is well known (Toporkova, 1973; Stumpel, 1985; Gruodis, 1987; Pikulik et al., 1988). Within Latvian forests, *A. fragilis* prefers dry or artificially drained pine-dominated stands, and avoids damp stands and mires (Čeirāns, 2002a, 2004). Multiple regression analysis did not reveal a preference for dry coniferous forests, probably due to peculiarities of the wet coniferous forest type in the survey. This latter habitat type also included artificially drained stands, which are also good habitat for *A. fragilis* (Čeirāns, 2004). *Anguis fragilis* was the only species of reptile in which an agricultural development adversely affected abundance. However, this species is still the second most abundant reptile in Latvia and it is unlikely that agriculture poses a threat to its persistence, for several reasons. First, the density of the rural population in Latvia is relatively low (<15 inhabitants per $km^2$) and has been steadily decreasing since World War II due to a population flow into cities (Overview of the Latvian indicators of sustainable development, 2003). Second, the percentage of agricultural lands also has been declining since the 1940s (Berkgaute et al., 1999). Finally, pollutant emissions, loads of fertilizers and pesticides in Latvia are relatively low, and have decreased by 80 – 90% since the early 1990s due to the economic depression following the collapse of the USSSR (Berkgaute et al., 1999; Fammler et al., 2000).

Other kinds of habitat loss or degradation are likely to be the biggest threats to most species of reptiles in Latvia. For example, the most important economic activity in many rural areas is timber harvesting, which increased two-fold between 1992 and 1997 (Berkgaute et al., 1999). However, harvesting is carried out mainly in mature stands, and for many reptile species its effect is positive rather than adverse, due to the creation of a more open mosaic habitat (Kutt, 1993; Blouin-Demers and Weatherhead, 2001; Lima et al., 2001). Raised bogs can be important habitats for some species and their loss can cause population decline (Phelps, 1978; Stumpel, 1992; Zuiderwijk et al., 1998). However, peat extraction in Latvia has significantly decreased since the early 1990s, with about 70% of bogs having been relatively untouched by human activities as recently as 1997 (Berkgaute et al., 1999). Some human activities in bogs, such as partial drainage, can even be beneficial for reptiles (Čeirāns, 2004). Thus, although these anthropogenic factors may be important locally, they are not likely to cause a large-scale reptile declines in Latvia.

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