On the importance of tree stand composition and age in forest habitats of *Anguis fragilis*, *Zootoca vivipara*, and *Natrix natrix* (Squamata: Sauria: Anguidae, Lacertidae; Squamata: Serpentes: Colubridae)

**Zur Bedeutung von Alter und Zusammensetzung des Baumbestandes in Waldlebensräumen von Anguis fragilis, Zootoca vivipara und Natrix natrix** (Squamata: Sauria: Anguidae, Lacertidae; Squamata: Serpentes: Colubridae)

**ANDRIS ČEIRĀNS**

**KURZFASSUNG**


**ABSTRACT**

Material on the forest habitats of reptiles was collected along with the making of inventories of the herpetofauna of two National Parks in Latvia: Kemeri National Park (1994-1997), and Gauja National Park (1998-2000). Information on the composition and age of stands of trees inhabited by reptiles was obtained from the database of the State Forest Service.

*Anguis fragilis* showed a preference for pine-dominated stands. The species avoided wetland forests. *Zootoca vivipara* preferred pine-dominated stands, and avoided deciduous stands. Data showed a negative correlation between the relative abundance of spruce and the age in stands inhabited by *Z. vivipara*. This species utilized spruce-dominated stands that were less than 40 years old, but avoided older stands. *Natrix natrix* showed no preference for any tree species in the forest habitats of the Kemeri National Park. Data on this species from the Gauja National Park was insufficient for analysis. There was a positive correlation between the relative abundance of deciduous trees and the age of stand inhabited by this species. All of the reptile species showed seasonal variation in the habitat utilization. Although relatively weak, statistically significant relationships were found for *A. fragilis* and *Z. vivipara* regarding their seasonal habitat preferences: pine was more typical for the spring and end of summer/autumn reptile habitats, and spruce and deciduous trees for summer habitats.

**KEY WORDS**

Reptilia: Squamata, Sauria, Anguidae, Anguis fragilis, Lacertidae, Zootoca vivipara; Serpentes, Colubridae, Natrix natrix, ecology, habitat selection, forest, tree stand, Latvia

**INTRODUCTION**

Large areas in Eastern Europe are still covered by forest. Forests occupy 44.7% of the territory of Latvia (Priedītis 1999), and all native reptile species, with the exception of *Emys orbicularis* (Linnaeus, 1758), can be found in forest habitats. All reptile species are ectotherms, and sun-exposure of habitat is one of the key factors that deter-
mines site utilization (Heatwole 1977). The sun-exposure of the understory in a forest depends on canopy features, such as species composition, canopy cover, stage of succession etc. Hence, the tree canopy in a forest strongly determines also the composition and structure of whole shrub and understory vegetation. For example, surface in coniferous forests has stable sun exposure during a whole vegetation season. Surface in a pine forest usually is well lit, but in a spruce forest – shaded, and these forests have different understory vegetation. Surface in a deciduous forest is subject to varying sun-exposure during a vegetation season, being well lit in spring, shaded in summer. As a result, there are considerable seasonal changes in understory vegetation (Priedtītis 1999).

In Western Europe, the role of the herb layer vegetation has been investigated in great details for several species, e.g., Lacerta agilis Linnaeus, 1758 and Zootoca vivipara (Jacquin, 1787) (House & Spellerberg 1983; Strubosch 1986; Dent & Spellerberg 1987; Spellerberg 1989). However, these investigations were made mainly in sites with relatively high reptile density, usually open habitats, but not in forest habitats. In Eastern Europe, data regarding the forest habitats of reptiles are either brief notes on sites of separate finds (e.g., Bondarenko & Starkov 1989; Dunaiev & Haritonov 1989), or densities in a forest dominated by one or another tree species (e.g., Pikulik et al. 1988). This information does not precisely indicate the sites preferred by reptiles, and it omits the role of forest succession.

In the 1990s, inventories of the herpetofauna of two large protected areas in Latvia - the Ķemeri National Park and the Gauja National Park was carried out. Three reptile species - the Slow Worm, Anguis fragilis Linnaeus, 1758, the Common Lizard Zootoca vivipara, and the Grass Snake Natrix natrix (Linnaeus, 1758), were regularly found there in forest habitats. Data on the location of sites, together with brief habitat descriptions, were collected. Forest inventories of stand structure have been carried out in both of the National Parks. Therefore it was possible to use the State Forest Service databases to study the relationship between tree stand parameters and reptiles. The present analysis was focussed on the composition and age of tree stands in sites utilized by reptiles. This type of analysis could be important for conservation purposes, allowing to predict utilization of sites by reptiles from forest databases. The predictions could be very useful for planning of protected areas, since two of these reptile species (A. fragilis, N. natrix) are unevenly distributed and relatively rare for Latvia (A. Čeirāns, unpublished).

**STUDY AREAS, MATERIALS AND METHODS**

Čemeri National Park (KNP)

The Ķemeri National Park was established in 1997, uniting several small areas that were under protection since 1962-1977. Most of the National Park is located in the Coastal Lowland south - southwest from the Gulf of Riga. Marginal areas in the southern part of the National Park are in the Zemgale Lowland, and the northwestern part is located in the North Kurzeme Upland. The total area of the Ķemeri National Park is 42,790 ha. Forests occupy 51%, mires 24%, waters 10%, agricultural lands and shrubs 12% and human settlements 3% of the territory (Latvian Fund for Nature, unpublished). The climate is moderately warm and moist (table 1).

Habitats are very diverse, containing the full range of forest types, found in Latvia. Both natural and disturbed forest areas can be found (Latvian Fund for Nature, unpublished). In coastal areas and on inland dunes, dry pine and pine-spruce forests are the most characteristic. Almost undisturbed wet black alder forests and swamps are situated along the Lielupe River and to the west of Lake Kaņieris. There are several large raised bogs in the National Park (Ķemeru-Smārdes Mire 6192 ha, Zaļais Mire 1586 ha, Raganu Mire 1274 ha etc.), and some smaller (Labais and Kasku Mires) of transitional bogs (Kavacs 1995). These mire areas are bordered by wide belts of wet or drained coniferous and deciduous forests.
Table 1: Climate characteristics for the Kemeri National Park and the Gauja National Park, Latvia (from Kavacs 1995, 1998). Ranges represent regional differences within each park.


<table>
<thead>
<tr>
<th>Climate characteristics</th>
<th>KNP (Kemeri National Park)</th>
<th>GNP (Gauja National Park)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Altitude (m a.s.l.)</td>
<td>0 – 72</td>
<td>25 – 174</td>
</tr>
<tr>
<td>Höhenlage (m üNN)</td>
<td>6 – 8</td>
<td>5 – 6</td>
</tr>
<tr>
<td>Mean annual temperature (°C)</td>
<td>Mittlere Jahrestemperatur (°C)</td>
<td>6 – 8</td>
</tr>
<tr>
<td>Mean temperature in January (°C)</td>
<td>Mittlere Januartemperatur (°C)</td>
<td>-4 – -5</td>
</tr>
<tr>
<td>Mean temperature in July (°C)</td>
<td>Mittlere Julitemperatur (°C)</td>
<td>17</td>
</tr>
<tr>
<td>Sum of active temperatures (°C)</td>
<td>Aktivitätstemperatursumme (°C)</td>
<td>1850 – 2000</td>
</tr>
<tr>
<td>Period with positive temperatures (days)</td>
<td>Anzahl frostfreier Tage</td>
<td>150 – 160</td>
</tr>
<tr>
<td>Annual Precipitation (mm)</td>
<td>700 – 800</td>
<td></td>
</tr>
<tr>
<td>Jährliche Niederschlagsmenge (mm)</td>
<td>700 – 800</td>
<td></td>
</tr>
</tbody>
</table>

Zootoca vivipara and *N. natrix* are common species that inhabit diverse habitats of the Kemeri National Park. *Anguis fragilis* is fairly frequent in dry and drained forests.

Gauja National Park (GNP)

The Gauja National Park was established in 1973. It is located in the north-central Latvia. The area is dissected by the ancient valley of the River Gauja (0.9-2.5 km wide, and up to 85 m deep) together with valleys of its numerous tributaries and side ravines. Different parts of the National Park belong to the Idumeja and Central Vidzeme Uplands, and the Tālava Lowland. The total area of the Gauja National Park is 91,745 ha. Forests occupy about 50%, agricultural lands and human settlements about 40% of the area. There is only one large mire, (Sudas-Zviedru Mire, 2575 ha, mainly a raised bog type) that is located in the southern part of the National Park (Kavacs 1995). The climate is moderately cool and moist (table 1).

The most common stands are dry pine-spruce forests, but deciduous and spruce forests occur on slopes of ravines and ancient valley of the Gauja River. There is considerable area of old broad-leaved forest near the town of Sigulda. Osier stands are characteristic for the flood plaine of the Gauja River. Wet coniferous forest areas are found around the Sudas-Zviedru Mire, and several wetland forest areas are also located in other parts of the Gauja National Park. Agricultural landscapes, although they occupy a large part of the National Park, are fragmented by many forest stands, shrubs, and fallow lands (Kavacs 1995).

Zootoca vivipara is a common species in the whole territory. *Anguis fragilis* and *N. natrix* are relatively rare species, with the former being confined mostly to dry coniferous forest areas, and the latter having a local distribution (various habitats mostly in the south-western part of the National Park).

Data collection and analysis

Data were collected during the inventory of herpetofauna in the field seasons (late April to early September) of 1994-1997 for the Kemeri National Park, and 1998-2000 for the Gauja National Park. The total length of transects in the forest habitats was 183.8 km in the former, and 98.6 km in the latter. Transects covered the whole territories and were evenly distributed. Therefore, in both cases, transects covered all of the main forest types in the same proportion as they are present in the Park. Censuses were carried out once on each transect, during 5-9 hours under dry and warm weather conditions. Each observation of a reptile was mapped at a scale of 1 : 50 000, and a brief description of the site was made. For further analysis, only observations within forest
Table 2: Number of forest stands analyzed in the Kemeri National Park and the Gauja National Park, Latvia.
Tab. 2: Die Anzahl der analysierten Baumbestände in den Nationalparks von Kemeri und Gauja, Lettland.

<table>
<thead>
<tr>
<th>Forest stands in sites of records of Gehölzbestände im Bereich von Vorkommen von</th>
<th>KNP (Kemeri National Park)</th>
<th>GNP (Gauja National Park)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anguis fragilis</td>
<td>14</td>
<td>8</td>
</tr>
<tr>
<td>Zootoca vivipara</td>
<td>28</td>
<td>21</td>
</tr>
<tr>
<td>Natrix natrix</td>
<td>22</td>
<td>3</td>
</tr>
<tr>
<td>Random stands / zufällig gewählte Vergleichsstandorte</td>
<td>200</td>
<td>200</td>
</tr>
</tbody>
</table>

stands (cuttings, path sides, under the gaps in the canopy etc.) were used. Observations on forest edges that bordered with open landscape are omitted, because such sites do not reflect the forest environment.

Each reptile site description made in the field was later compared with forest management plans and stand descriptions from the database of the State Forest Service, to ensure coherence between both the find and database. Composition and age of each forest stand inhabited by reptiles was determined from the forest database. Two reptile observations were considered to be separate, if they were located in different forest stands. In this case a stand is defined as an area on a forest management plan that differs in situation from neighbouring areas.

I used randomly selected stands from the State Forest Service database (200 for each of the study areas) as random sites for comparison with stands inhabited by reptiles. The number of analyzed stands for each reptile species is shown in table 2. The data set for *N. natrix* from the Gauja National Park was too small for separate analysis, and it was used only in the analysis of the variation of preferred habitats during a season.

Data base of the State Forest Service

Forest data bases are created by professionals during inventory of forest stands for forestry purposes. Forest inventory was carried out in the Kemeri National Park in 1989 and in the Gauja National Park mainly in 1987-1988 (some territories were inventorized in 1994). The data base is supplemented by forest plans at scale 1 : 20 000. The forest is divided into stands with uniform growth conditions and tree stand features. The area occupied by a stand varied from less than 0.5 ha to more than 15 ha.

Only a few stand parameters from the forest databases appeared to be useful for the present scientific purposes. Some of the parameters, such as standing volume, origin of stand etc., are useful mainly for forest management. The mean heights and diameters of trees indicated in the database are misleading (especially regarding young stands) due to the long time span between the inventory of stand and reptile observations (5-8 years for the Kemeri National Park, and 5-13 years for the Gauja National Park). However, the exact age of the stand can be calculated from the database, and the tree species composition of the stand from the database can be used with a sufficient level of confidence.

The mean age of stands has been determined from cores bored from the root neck in several medium sized trees. The stand composition in the data base is characterized by a code, where each tree species has a coefficient (an integer between 1 and 10) proportional to the stock of each species in the stand. The tree species for which stocking is less than 5 % are not included in the formula. The sum of coefficients of all components is 10 (Brice 1998). In the present analysis, coefficients for all deciduous species were pooled.

Statistics

Differences in age and composition of the tree stands were assessed by the non-parametric Mann-Whitney (Wilcoxon) test. Simple linear regression analysis was performed to test the relationship between age and proportion of various tree species in the various stands. Polynomial regression anal-
Table 3: Age (in years) of forest stands inhabited by *Anguis fragilis*, *Zootoca vivipara*, *Natrix natrix*, and of random stands (mean ± standard error, range in parentheses).

<table>
<thead>
<tr>
<th>Forest stands in sites of records of Gehölzebestände im Bereich von Vorkommen von</th>
<th>KNP (Ķemeri National Park)</th>
<th>GNP (Gauja National Park)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Anguis fragilis</em></td>
<td>81.4 ± 5.4 (47-112)</td>
<td>95.1 ± 15.6 (37-164)</td>
</tr>
<tr>
<td><em>Zootoca vivipara</em></td>
<td>59.6 ± 6.5 (10-147)</td>
<td>70.4 ± 7.0 (15-114)</td>
</tr>
<tr>
<td><em>Natrix natrix</em></td>
<td>68.6 ± 4.4 (24-97)</td>
<td>----</td>
</tr>
<tr>
<td>Random stands / zufällig gewählte Vergleichsstandorte</td>
<td>70.8 ± 2.2 (7-182)</td>
<td>79.2 ± 2.4 (13-194)</td>
</tr>
</tbody>
</table>

Analysis was used to test the statistical significance of relationship between reptile observation date and stand composition, fitting of second and third order polynomial model was tested. All statistical analyses were performed using STATGRAPHICS Plus 2.1® software on a Microsoft® operating system.

**RESULTS**

*Anguis fragilis*

Forest stands inhabited by *A. fragilis* were older than randomly chosen sites (table 3), but the differences were not significant (KNP *p* = 0.45, GNP *p* = 0.31). Pine (*Pinus sylvestris*) was the dominant species in habitats of *A. fragilis* (tables 4-5). Relative abundance differences from random sites were significant at both study areas (KNP *p* = 0.02, GNP *p* = 0.04). Spruce (*Picea abies*) and deciduous trees usually had low relative abundance in *A. fragilis* habitats, with a few exceptions for drained areas in the Kemeri National Park.

Birch (*Betula pendula, B. pubescens*) was the main deciduous tree in stands inhabited by *A. fragilis* in the Kemeri National Park (mean coded proportion in stands 1.79), and the only deciduous tree species in the habitats of the Gauja National Park. Other deciduous species (*Alnus glutinosa, Fraxinus excelsior, Populus tremula, Quercus robur*) were far less important.

*Zootoca vivipara*

Forest stands inhabited by *Z. vivipara* were younger than randomly chosen sites (table 3). These differences were significant in the Kemeri National Park (*p* = 0.01), but not in the Gauja National Park (*p* = 0.53).

Concerning its habitat preferences, the species behaved different in the two study areas. In the Gauja National Park, pine (*Pinus sylvestris*) strongly dominated in the habitats (table 5), it was preferred over other trees (relative abundance differences comparing with random sites: *p* = 0.03). There was no difference in composition between young and mature stands utilized by *Z. vivipara*.

In the Kemeri National Park, *Z. vivipara* habitats were more variable, and their stands composition was correlated to age (table 4). Both pine and spruce (*Picea abies*) prevailed in the *Z. vivipara* habitats. However, differences in relative abundance from random sites were not significant for both pine (*p* = 0.25), and spruce (*p* = 0.24). Old spruce-dominated stands were avoided (see discussion). Correspondingly, the proportions of pine and deciduous trees tended to increase in mature stands inhabited by *Z. vivipara*.

Deciduous tree stands were avoided comparing with random sites (*p* = 0.004). The most important deciduous trees in stands inhabited by *Z. vivipara* were birch species (mean coded proportion in Kemeri NP – 1.36, in Gauja NP – 1.76). Other deciduous tree species (*Populus tremula, Quercus robur, Alnus glutinosa, Fraxinus excelsior, Salix sp., Alnus incana, Ulmus sp.*) were rare.
Table 4: Kemeri National Park. Stand composition (coded by formula from the database of the State Forest Service) and correlation between the proportion of various stand components and the age of the stands \((r, p)\) in places inhabited by reptiles, and in random sites. ** - significant at \(p < 0.05\); * - significant at \(p < 0.1\).

<table>
<thead>
<tr>
<th>Habitat of Fundort von</th>
<th>Tree species</th>
<th>Mean (\pm) Standard Error</th>
<th>Range Spannweite</th>
<th>(r)</th>
<th>(p)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anguis fragilis</td>
<td>Pine / Föhre</td>
<td>6.43 (\pm) 0.97</td>
<td>0 - 10</td>
<td>0.10</td>
<td>0.75</td>
</tr>
<tr>
<td></td>
<td>Spruce / Fichte</td>
<td>1.36 (\pm) 0.55</td>
<td>0 - 6</td>
<td>-0.07</td>
<td>0.80</td>
</tr>
<tr>
<td></td>
<td>Deciduous trees / Laubbäume</td>
<td>2.21 (\pm) 0.76</td>
<td>0 - 9</td>
<td>-0.07</td>
<td>0.81</td>
</tr>
</tbody>
</table>

Zootoca vivipara

| Pine / Föhre | 5.14 \(\pm\) 0.74 | 0 - 10 | 0.47** | 0.01 |
| Spruce / Fichte | 3.29 \(\pm\) 0.76 | 0 - 10 | -0.65** | 0.0002 |
| Deciduous trees / Laubbäume | 1.57 \(\pm\) 0.39 | 0 - 8 | 0.37* | 0.05 |

Natrix natrix

| Pine / Föhre | 4.68 \(\pm\) 0.87 | 0 - 10 | -0.19 | 0.39 |
| Spruce / Fichte | 1.55 \(\pm\) 0.50 | 0 - 10 | -0.26 | 0.23 |
| Deciduous trees / Laubbäume | 3.77 \(\pm\) 0.73 | 0 - 10 | 0.41* | 0.06 |

Random stands

| Pine / Föhre | 4.13 \(\pm\) 0.28 | 0 - 10 | 0.29** | 0.0000 |

Zufällig gewählte Vergleichsstandorte

| Spruce / Fichte | 1.95 \(\pm\) 0.19 | 0 - 10 | -0.26** | 0.0002 |

Vergleichsstandorte

| Deciduous trees / Laubbäume | 3.92 \(\pm\) 0.26 | 0 - 10 | -0.12* | 0.09 |

There were no differences in age of tree stands between habitats of \(N. natrix\) and randomly chosen sites \((p = 0.29)\) (table 3), and species did not show a preference for a tree species (table 4). Young deciduous stands were avoided by \(N. natrix\) (see discussion). Unlike the two previous reptile species, \(N. natrix\) often inhabited stands with a large proportion of deciduous trees. The most important deciduous component in stands inhabited by \(N. natrix\) was birch (mean coded proportion 2.68), while broad-leaved trees (\(Alnus glutinosa - 0.72\), \(Fraxinus excelsior - 0.23\)) and aspen (\(Populus tremula - 0.14\)) were less important.
Table 6: Statistical significance ($p$) in the relationship between proportion of tree species in the reptile habitat and reptile observation date. For each reptile species are indicated: fitting at second order polynomial model ($R^2$ in the first row), and fitting at third order polynomial model ($R^2$ in the second row). ** - significant at $p < 0.05$; * - significant at $p < 0.1$.

Die statistische Signifikanz ($p$) des Zusammenhangs zwischen dem Anteil der Baumarten und dem Datum der Kriechtierbeobachtungen. Angegeben sind für jede Kriechierart die Anpassung des Polynommodells zweiter Ordnung ($R^2$ in der ersten Reihe) und die Anpassung des Polynommodells dritter Ordnung ($R^2$ in der zweiten Reihe). Signifikanzniveaus: ** - $p < 0.05$; * - $p < 0.1$.

<table>
<thead>
<tr>
<th>Forest stands in places of records of Gehölzbestände im Vorkommensbereich von</th>
<th>Pine</th>
<th>Spruce</th>
<th>Deciduous trees</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Anguis fragilis</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$R^2 = 0.20, p = 0.13$</td>
<td>$R^2 = 0.07, p = 0.50$</td>
<td>$R^2 = 0.15, p = 0.22$</td>
<td></td>
</tr>
<tr>
<td>$R^2 = 0.36*, p = 0.06$</td>
<td>$R^2 = 0.08, p = 0.70$</td>
<td>$R^2 = 0.34*, p = 0.05$</td>
<td></td>
</tr>
<tr>
<td><strong>Zootoca vivipara</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$R^2 = 0.08, p = 0.16$</td>
<td>$R^2 = 0.05, p = 0.29$</td>
<td>$R^2 = 0.05, p = 0.35$</td>
<td></td>
</tr>
<tr>
<td>$R^2 = 0.17**, p = 0.04$</td>
<td>$R^2 = 0.25**, p = 0.005$</td>
<td>$R^2 = 0.06, p = 0.40$</td>
<td></td>
</tr>
<tr>
<td><strong>Natrix natrix</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$R^2 = 0.13, p = 0.22$</td>
<td>$R^2 = 0.002, p = 0.98$</td>
<td>$R^2 = 0.14, p = 0.19$</td>
<td></td>
</tr>
<tr>
<td>$R^2 = 0.14, p = 0.35$</td>
<td>$R^2 = 0.10, p = 0.54$</td>
<td>$R^2 = 0.14, p = 0.35$</td>
<td></td>
</tr>
</tbody>
</table>

Seasonal variations in habitat preferences by reptiles

Microclimatic conditions on the ground surface differ depending on canopy composition, and seasonal variations in habitat preferences by reptiles can be expected. In this respect, I observed monthly variations in the mean proportion of stand components (figs. 1-3). The data set was too small for separate analysis for each of the study areas, and data from both were combined.

All three reptile species showed two peaks - (i) spring and (ii) end of summer / autumn for the selection of pine-dominated stands. The relationship between the relative abundance of pine and the date was relatively weak, but statistically significant for *Anguis fragilis* and *Zootoca vivipara* (table 6). Spruce was at maximum in *Zootoca vivipara* summer habitats; this relationship was weak, but significant. No distinctive pattern regarding the presence of spruce in a habitat was found in the other two reptile species.

There was no evidence of preferred utilization of deciduous stands by reptiles in spring, when the forest ground is well lit. Moreover, in the meteorological summer month June, the average proportion of deciduous tree stands utilised as habitat by *Anguis fragilis* was higher than in May (fig. 1); this relationship was relatively weak, but significant. A similar trend (but statistically not significant) was observed in *Natrix natrix* habitats (fig. 3).

**DISCUSSION**

*Anguis fragilis* habitats

My data showed that, in Latvia, *A. fragilis* prefers pine forests. In several cases the species was observed in mixed or deciduous stands usually bordering with pine forest. The species is referred to be quite sedentary, with a home range of 250-400 square meters (Speellerberg 1988). There was weak correlation between observation date and canopy composition (table 6), and hence some migration between habitats can be suggested.

The species was found in older stands than random samples, although the differences were not statistically significant. Considering also the sedentary habit of *A. fragilis*, this may indicate that the species is more sensitive to habitat disturbances than are other reptiles. *Anguis fragilis* avoided wet habitats. It was found in dry stands in 16 cases, and in former wet stands that have been ditched - in 6 cases. In several cases, the drained sites were not in contact with historically dry habitats.
Fig. 1: Monthly variation in the composition of the stands of trees utilized by *Anguis fragilis*.
Abb. 1: Monatliche Schwankung in der Zusammensetzung des von *Anguis fragilis* besiedelten Gehölzbestandes.

Fig. 2: Monthly variation in the composition of the stands of trees utilized by *Zootoca vivipara*.
Abb. 2: Monatliche Schwankung in der Zusammensetzung des von *Zootoca vivipara* besiedelten Gehölzbestandes.

Fig. 3: Monthly variation in the composition of the stands of trees utilized by *Natrix natrix*.
Abb. 3: Monatliche Schwankung in der Zusammensetzung des von *Natrix natrix* besiedelten Gehölzbestandes.
Information from other East European countries on forests inhabited by *A. fragilis* is scanty. However, data from Lithuania (GRUODIS 1987) and northern Belarus (PIKULIK et al. 1988) confirm that both young and mature dry pine forest is the most typical forest habitat for *A. fragilis* in the boreo-nemoral zone.

*Anguis fragilis* is a secretive species. Hence, domination of pine in the canopy which allows good sun-exposure of the surface layer, could be one of the main factors that determine the presence of *A. fragilis* in the forest habitats of Latvia.

*Zootoca vivipara* habitats

*Zootoca vivipara* avoided spruce-dominated (> 5) stands that were more than 40 years old (fig. 4-top), and such stands were well represented at the study areas (fig. 4-bottom). The only exception was a mature spruce-dominated stand in the Gauja National Park, where the species was found about 30 m from a neighbouring pine-dominated stand. Young spruce stands, which are often thinned to produce higher wood volume from each tree (BRICE 1998), are good *Z. vivipara* habitats until canopy closure. At
the age of 35-45 years, spruce is about 10-15 m high with a mean stem diameter of 11-16 cm at 1.3 m height (data from the State Forest Service database). At these ages, stands become too shaded to sustain *Z. vivipara* populations. The positive effect of stand thinning in forests has been observed for heliothermic lizards in Australia (Kutt 1993) and South America (Lima et al. 2001).

Spruce was far more typical for *Z. vivipara* habitats in the Ķemeri National Park than in the Gauja National Park. In a random data set, the proportion of spruce dominated stands that were younger than 40 years was 5.0% of all stands in the Ķemeri National Park and 2.2% in the Gauja National Park. In the Ķemeri National Park, many areas have been planted, logged, and thinned as this Park was only recently established. Hence differences between both study areas could result from the rarity of young open spruce stands suitable for *Z. vivipara* in the Gauja National Park. However, climate differences between both areas (table 1) can also explain the results (see below).

Pine-dominated stands of various ages were typical forest habitats of *Z. vivipara* in both study areas, and deciduous stands were avoided. In the southern and eastern parts of the boreo-nemoral forest zone, utilization of
deciduous stands by *Z. vivipara* is more usual (PIKULIK et al. 1988; DUNAJEV & HARITONOV 1989). In northern Belarus (Valley of River Zapadnaja Dvina), the average density of *Z. vivipara* in deciduous forests was observed to be 3 - 4 times lower than in pine forests (PIKULIK et al. 1988). In central Belarus (Berezina Reserve), *Z. vivipara* inhabited deciduous stands, but avoided dry pine forest. Pine forests there were utilized by *L. agilis* (PIKULIK et al. 1988). Similarly, some regional variations in the habitats of *Z. vivipara* in Latvia can be expected.

**Natrix natrix** habitats

*Natrix natrix* in forest habitats of Latvia showed no preference of any tree species. The snake has high dispersal ability, a wide range of seasonal movements, and a large home range size. The mean daily range of movement varies from 13 to 114 m depending on season and sex, and the mean monthly home range size is 10-14 ha (MADSEN 1984). Factors other than the species composition of the canopy apparently determine the presence of *N. natrix* in forest habitats. Such factors could be the presence of suitable incubation, wintering and basking sites, moisture conditions in the habitat, the presence of water bodies and amphibian populations, protection from predators etc. (PHELPS 1978; MADSEN 1984; SPELLERBERG 1988; BONDARENKO & STARKOV 1989; DROBENKOV 1995).

However, some canopy features have been observed to be important. In my study, mature deciduous stands were preferred over young stands. *Natrix natrix* was not found in stands dominated by deciduous trees that were younger than 45 years (fig. 5-top), and such stands were present in a random sample (fig. 5-bottom). A similar relationship with age of stand was also observed for *Z. vivipara* in the same area (Kemeri National Park) (table 4). Deciduous trees (*Betula* sp., *Populus tremula*, *Alnus incana*) rapidly regenerate on clearings and fallow-lands, and in Latvia, unlike coniferous stands, deciduous stands have seldom been artificially planted and thinned (BRICE 1998). Hence, the surface in young deciduous stands is shaded. In mature deciduous forest, surface is better exposed to light due to natural gap disturbance (PRIEDITIS 1999).

In the Eastern European boreo-nemoral zone, *Natrix natrix* is considered to inhabit diverse forests, where moist deciduous stands being more typical for the species (GRUODIS 1987; PIKULIK et al. 1988; BONDARENKO & STARKOV 1989; DUNAJEV & HARITONOV 1989). My data showed no preference for deciduous stands by *N. natrix* in Latvia. This can be explained by the presence of large wet forest areas with a network of drainage ditches in the study area. Eighteen of 22 sites inhabited by *N. natrix* were in wetland or drained forests, both deciduous and coniferous.

**CONCLUSION**

The composition and age of stands of trees were shown to affect reptile habitat choice in Latvian forests. Pine in stands of various ages was preferred over other tree species by *A. fragilis* and *Z. vivipara*. The former reptile species avoided wetland forests, but was present in drained sites. Young spruce stands were often used by *Z. vivipara*, but mature stands dominated by spruce were usually avoided. Stands with large proportion of deciduous trees were avoided by both *A. fragilis* and *Z. vivipara*, but utilized by *N. natrix*. *Natrix natrix* showed preference of mature deciduous stands over young ones. Some seasonal variations in utilization of forest by reptiles were observed. The highest proportion of pine in habitats of all three species was in spring and in late summer to autumn. The cover of spruce and deciduous trees, which provide more shadow than pine, tended to increase in reptile habitats in summer.
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