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Reptiles in sub-boreal forests of Eastern Europe: patterns of forest type preferences and habitat use in *Anguis fragilis*, *Zootoca vivipara* and *Natrix natrix*
(Squamata: Sauria: Anguidae, Lacertidae; Serpentes: Colubridae)

Kriechtiere im subborealen Wald Osteuropas: Präferierte Waldtypen und Habitatnutzung bei *Anguis fragilis*, *Zootoca vivipara* und *Natrix natrix*
(Squamata: Sauria: Anguidae, Lacertidae; Serpentes: Colubridae)

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KURZFASSUNG

In zwei Nationalparks in Lettland (im Nationalpark von Ķemeri 1994-1997 und im Nationalpark von Gauja 1998-2000) wurden Daten über Waldlebensräume von Reptilien gesammelt. Die Klassifikation der Waldlebensräume erfolgte auf Grundlage der Typologie lettischer Wälder, die auf Standorteigenschaften basiert. Berechnet wurden für jeden Waldtyp die Abweichungen von den erwarteten Werten der Reptiliennachweise sowie die Nischenbreite und -überlappung der Reptilienlebensräume. Drei Kriechtierarten - *Anguis fragilis* LINNAEUS, 1758, *Zootoca vivipara* (JACQUIN, 1787) und *Natrix natrix* (LINNAEUS, 1758) - kamen in den Waldlebensräume regelmäßig vor. *Anguis fragilis* wurde ausschließlich in trockenen und entwässerten Wäldern beobachtet, *Z. vivipara* und *N. natrix* besiedelten die unterschiedlichsten Waldtypen. Für die genannten Arten werden die Präferenzen gegenüber bestimmten Waldtypen und das Ausmaß der Überlappung ihrer Lebensräume diskutiert.

ABSTRACT

Material on the forest habitats of reptiles was collected in two National Parks of Latvia: Ķemeri National Park (1994-1997), and Gauja National Park (1998-2000). Habitats were classified according to the Latvian forest typology that focuses on site quality of the stand. Deviations from the expected proportions of reptile records for each forest type, niche breadth and overlap of the reptile habitats were determined. Three reptile species - *Anguis fragilis* LINNAEUS, 1758, *Zootoca vivipara* (JACQUIN, 1787), *Natrix natrix* (LINNAEUS, 1758) - were common in forest habitats. *Anguis fragilis* was observed in dry or drained forest only, *Z. vivipara* and *N. natrix* inhabited various forest types. Preferences for forest types and the pattern of habitat overlap for these species are discussed.

KEY WORDS

Reptilia: Squamata: Sauria, Anguidae, *Anguis fragilis;* Lacertidae, *Zootoca vivipara*; Serpentes, Colubridae, *Natrix natrix*, ecology, habitats, habitat niche breadth and overlap, palearctic sub-boreal forest, Latvia

INTRODUCTION

Forest was the most characteristic European landscape feature beginning from the early post-glacial era, when about 80-90% of the territory was forested, till the Middle Ages when large-scale deforestation commenced in Central Europe. Presently, forest still covers about 312 million hectares (33%) of Europe, mostly in the Nordic and East European countries (STANNERS & BOURDEAU 1995).

Unlike the Nordic Countries, where the intensification of forestry (e.g., using mechanization in forest planting and harvesting, the use of fertilizers, monoculture planting) resulted in considerable loss of biodiversity, the forests of East Europe have remained less affected (STANNERS & BOURDEAU 1995)

Therefore, reptile studies in East European forests are important from several aspects. The first is to gain understanding of how widely reptiles exploit forest resources – the habitat that once dominated throughout most of the range of many native species. The other stems from the species conservation aspect – after the collapse of the Soviet Union and establishing the market economy in the former socialistic countries, threats to biodiversity are increasing in this area. Thus, it is important to survey the role of forest resource diversity for reptiles.

Information on reptile habitat preferences in the forests of East Europe is scanty, and mostly describes the density of reptiles in stands dominated by particular tree species (e.g., BELOVA 1976; GRUODIS 1987; PIKULIK et al. 1988). The main reasons for this lack of information are: i) low overall densities of reptiles in temperate forests (e.g., JĘDRZEJEWSKA & JĘDRZEJEWSKI 1998), and ii) use of mostly ephemeral microhabitats created by canopy gap disturbance (GREENBERG 2001) and use of ecotopes (e.g., PIKULIK et al. 1988). In Western Europe the role of forests as reptile habitats is largely overlooked, with few exceptions (e.g., SPELLERBERG 1988).

The aim of the present study was to determine the general pattern of spatial distribution of reptiles among major groups of sub-boreal wooded habitats (classified by stand composition, species composition in the herb layer, groundwater regime). Bogs were also included in the study due to the gradual transition from raised bogs covered with sparse trees to wet forests.

The present publication is the second on reptile habitats in two National Parks of Latvia – the Ķemeri National Park and the Gauja National Park – based on the studies carried out in 1994-2000. A previous publication (ČEIRĀNS 2002a) described the importance of tree stand composition and age for *Anguis fragilis* LINNAEUS, 1758, *Zootoca vivipara* (JACQUIN, 1787) and *Natrix natrix* (LINNAEUS, 1758) - three common reptile species in forests of those areas.

MATERIALS AND METHODS

Study areas

Ķemeri National Park (KNP) is located south-southwest of the Gulf of Riga. The total area is 42,790 ha; forests occupy 51%, mires 24%, waters 10%, agricultural lands and shrubs 12% and human settlements 3% of the territory. Altitude ranges from 0 to 72 m a.s.l, sum of active temperatures is 1850-2000 °C, annual precipitation is 700-800 mm (KAVACS 1995, 1998). Forest habitats are very diverse, containing the full range of forest types found in Latvia (Latvian Fund for Nature, unpublished).

Gauja National Park (GNP) is located in north-central Latvia. The total area is 91,745 ha, forests occupy ~ 50%, agricultural areas and human settlements ~ 40% of the territory, mires are few in number and extension. Altitude in the GNP ranges from 25 to 174 m a.s.l., sum of active temperatures is 1800-1900 °C, annual precipitation is 700-800 mm, and upland forests dominate in the area (KAVACS 1995, 1998). A more comprehensive description of the study areas has been published elsewhere (ČEIRĀNS 2002a).

Forest classification in Latvia

Latvia has a unique system of forest typology that does not emphasize phytosociological aspects, but focuses on site quality of particular land-types (AVIS 1997). Hence, this typology is designed manly for forestry purposes.

There are five major groups of forest types depending on water regime and trophic level, further subdivided into 23 growth condition types on the basis of their position along a nutrient and floral species composition gradient, from poor (oligotrophic) to rich (eutrophic) stands. Wet forests were divided in two groups: forests on mineral soil (periodically wet, roots of trees reach underlying mineral soil), and forests on wet peat (roots do not reach mineral soil). Similarly, drained forests were also divided into forests on drained mineral and drained peat soil (BUŠS 1997). There is a gradual transition with increasing paludification from pine forest on *Sphagnum* peat to raised bog (association Sphagnion magellanici, after KABUCIS 2000), where the role of moss in biomass accumulation is more important than the role of trees (BUŠS 1997). The characteristics of 20 forest types surveyed are shown in table 1.

The syntaxonomical classification of Latvian forests has not been fully developed yet, and has been applied only to natural forests. It has some similarity with forest typology, especially regarding upland pine forests, where three types (Cladinoso-callunosa, Vacciniosa, Myrtillosa) are coherent with plant associations. However, there are many substantial differences from forest typology also. Thus, a given plant association can be found in several forest types (in wet pine forests, for example), or several plant associations can be found in one forest type, especially regarding deciduous and spruce forests (Aegopodiosa, Myrtilloso-polytrichosa, Dryopteriosa, Filipendulosa types) (PRIEDĪTIS 1999). At present, this forest typology is the only forest classification system that covers the whole variety of Latvian forests.

In the present analysis two wet pine forest types (Sphagnosa, Caricoso-phragmitosa) were combined because they belong to same plant association (Vaccinio uliginosi-Pinetum) (PRIEDĪTIS 1999).

Data collection

Data were collected along transects in the field seasons (later April to early September) of 1994-1997 (Ķemeri National Park), and 1998-2000 (Gauja National Park). Transects were evenly distributed and covered the whole territory in both study areas. The total length of the transects was 198.1 km in KNP and 103.7 km in GNP. Eighteen forest and raised bog types were documented in KNP, and 11 in GNP (table 2). All but three forest types found in Latvia were covered by transects in one or the other study area, and these were the relatively rare types (BUŠS 1997): periodically wet sparse pine forests on very poor sandy soil (Callunoso-sphagnosa), post-drained Callunoso-sphagnosa type (Callunosa mel.), and wet black alder forests on woody peat in sites with abundant calcareous groundwater flow (Filipendulosa).

Censuses were carried out once on each transect, for 5-9 hours under dry and warm weather conditions. Transects were laid out mainly along path sides, cuttings, under canopy gaps and similar locations, with potentially highest reptile density. Each observation of a reptile was mapped at a scale 1: 50 000, and a brief description of the site was made. Each description 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 the database. In the case of discrepancy the record was omitted. Observations on forest edges and sides of large roads were excluded from analysis as not representing a forest environment. Observations of juveniles were also omitted to reduce seasonal variation in density. Forest types along transects were determined from the forest database.

Data analysis

Deviation (D) from the expected proportion of reptile records in each forest type was calculated by a simple formula:

$$D = (O - E) / E$$

where O is the observed proportion of records (%), and E the forest type proportion (%) on the transects. Values are between -1 and 0, if a species avoids a particular habitat and > 0 if a habitat is preferred. There is no applicable statistical method to test the significance of this deviation (D). However, the representativeness of a given transect in a particular forest corresponds to the length of the transect due to low overall density of reptiles in temperate forests. Hence, the significance of the deviation (D) was evaluated by transect length with the most plausible results for transect lengths of more than 10 km, and the least plausible results for transects of less than 2 km (table 2).

Two formulas were used to evaluate the species niche breadth in forests. In the case of wide niche breadth, the proportional exploitation of all forest types was to be expected. The sum of absolute numbers from deviations of expected record proportions (observed proportion (%) of record minus forest type proportion) approaches 0 in case of total correspondence and 200 in case of total discrepancy with the distribution of forest types on site. Therefore niche breadth (NB) could be expressed by the formula

$$NB = 1 - \left[\sum_{i=1}^{n} |O - E|\right] / 200$$

with values ranging from 1 (equal exploitation of all forest types) to 0. Levins's measure of niche breadth (NB_{Levins}) was also calculated (KREBS 1989):

$$NB_{Levins} = 1 / \sum_{i=1}^{n} p_i^2$$

Table 1: Characteristics (after BUŠS 1997) of forest types surveyed in Ķemeri National Park (KNP) and Gauja National Park (GNP) in Latvia.

Tab. 1: Charakterisierung (nach BUŠS 1997) der betrachteten Waldtypen in den lettischen Nationalparks von Ķemeri (KNP) und Gauja (GNP).

Forest type / Waldtyp	Description / Beschreibung
Natural upland (dry) forests / Natürliche, höher gelegene (trockene) Wälder	
Cladinoso-callunosa	Pine forests on dry and sandy soil with lichens (*Cladina, Cladonia, Cetraria*) on ground surface
Vacciniosa	Pine forests on fairly poor mineral soil where the herb layer is dominated by *Vaccinium vitis-idaea*
Myrtillosa	Pine forests (spruce only in subcanopy) where the herb layer is dominated by *Vaccinium myrtillus*
Hylocomiosa	Pine – spruce forests on mesotrophic soil with more diverse, but still *Vaccinium myrtillus* - dominated herb layer
Oxalidosa	Spruce (with birch and aspen) forests on mesotrophic soil where *Oxalis acetosella* is typical for herb layer
Aegopodiosa	Hardwood (with birch and spruce) forests on moist eutrophic soil with rich and diverse herb layers
Wet natural forests on mineral soil / Feuchte natürliche Wälder auf mineralischen Böden	
Vaccinioso-sphagnosa	Pine forest on poor soil with several *Vaccinium* species, *Calluna vulgaris*, *Ledum palustre* in the herb layer, and *Sphagnum* in the moss layer
Myrtilloso-sphagnosa	Pine-birch (spruce in subcanopy) forests on mesotrophic soil, the herb layer is dominated by *Vaccinium myrtillus*, the moss layer – by *Sphagnum*, *Polytrichum commune*
Myrtilloso-polytrichosa	Spruce-birch (with pine) forests on potentially productive soil, the herb layer is dominated by *Vaccinium myrtillus*, the moss layer – by *Sphagnum*, *Polytrichum commune*
Dryopteriosa	Birch (with spruce, ash, black alder) forests on potentially productive soil with rich and diverse herb layer
Wet natural forests on peat soil / Feuchte natürliche Wälder auf torfigen Böden	
Sphagnosa	Pine forests un oligotrophic *Sphagnum* peat, the herb layer is dominated by *Eriophorum vaginatum*, *Calluna vulgaris*, *Ledum palustre*
Caricoso-phragmitosa	Pine-birch forests (spruce in subcanopy) on mesotrophic *Carex-Sphagnum*-tree peat with several sedge (*Carex*) species in the herb layer, and *Vaccinium* on hummocks
Dryopterioso-caricosa	Birch-black alder (with spruce) forests on eutrophic tree-*Carex* peat with diverse and well developed herb and moss layers
Forests on drained mineral soil / Wälder auf entwässerten mineralischen Böden	
Vacciniosa mel.	Pine (with birch) forests on oligomesotrophic soil, pre-drained types – Vaccinioso-sphagnosa, *Molinia* meadows
Myrtillosa mel.	Pine-birch (spruce in subcanopy) forests on meseutrophic soil, pre-drained types – Myrtilloso-sphagnosa, Myrtilloso-polytrichosa, unforested wetlands
Mercurialiosa mel.	Spruce-birch (with ash, black alder) forests on eutrophic soil, pre-drained types – Dryopteriosa, wet meadows
Forests on drained peat soil / Wälder auf entwässerten torfigen Böden	
Callunosa turf. mel.	Pine forests on oligotrophic peat soil, pre-drained types – Sphagnosa, transitional raised bog with pine
Vacciniosa turf. mel.	Pine-birch forests on oligomesotrophic peat soil, pre-drained types – transitional swamp forests, Caricoso-phragmitosa with pine
Myrtillosa turf. mel.	Pine-spruce-birch forests on meseutrophic peat soil, pre-drained types - Caricoso-phragmitosa, potentially productive transitional bogs and fens
Oxalidosa turf. mel.	Spruce (with birch, ash, black alder, pine) forests on eutrophic peat soils, pre-drained types - Dryopterioso-caricosa, Filipendulosa, minerotrophic swamps

where p_i is the proportion of records in the i^{th} forest type of n forest types.

The percentage overlap (P_{jk}) and Hurlbert's index of niche overlap (L) (KREBS 1989) were used to evaluate the habitat overlap between reptile species.

The percentage overlap was calculated as

$$P_{jk} = [\sum_{i=1}^{n} (\text{minimum } p_{ij}, p_{ik})] * 100$$

and Hurlbert's index as

$$L_{jk} = \sum_{i=1}^{n} (p_{ij} * p_{ik} / a_i)$$

where p_{ij}, p_{ik} are the proportions (%) of the records of the species j and k in the forest type i and a_i is the proportion of forest type i in the transects.

Regression analysis was performed to test the relationship between transect length and number of records in the forest type. Statistical analyses were performed using Microsoft© STATGRAPHICS Plus 2.1® software.

RESULTS

A total of 149 reptile records were counted (86 in KNP, 63 in GNP). Two species – *Anguis fragilis* LINNAEUS, 1758 and *Zootoca vivipara* (JACQUIN, 1787) – out of five were regularly found in both of the study areas. As to *A. fragilis* records, mean density was the same in both study areas (0.08 records per km), while in *Z. vivipara* the mean density was more than two times higher in GNP than in KNP (0.48 and 0.21 records per km, respectively). Density in the latter was higher for most of the forest types, most likely due to differences in the activity of the species between years of data collection (1994-97 for KNP and 1998-2000 for GNP). *Natrix natrix* (LINNAEUS, 1758) was common in forests in KNP (0.13 records per km), but not in GNP (0.03 records per km), reflecting its uneven distribution and rarity (ČEIRĀNS 2002b). Two species – *Lacerta agilis* LINNAEUS, 1758, *Vipera berus* (LINNAEUS, 1758) – were rare in both areas (densities 0.01 or less records per km).

Anguis fragilis habitat preferences

The correlation between the number of *A. fragilis* records and the transect length by forest types was not significant for KNP (R^2 = 9.5%, p = 0.21) and positive for GNP (R^2 = 70.3%, p = 0.001).

Anguis fragilis was found more often than expected in two groups of forest types (table 2). Of the dry upland forests it preferred pine-dominated types on fairly poor to moderately rich soil (Vacciniosa, Myrtillosa). Data regarding mesotrophic forests of the Hylocomiosa type were discrepant. There were large percentages of *A. fragilis* observations in these forests for both of the study areas (KNP – 26.7%, GNP – 37.5%). However, in KNP the number of observations was higher than expected, but in GNP lower than expected. Hylocomiosa is a forest type where both pine and spruce can be dominant (BUŠS 1997). *Anguis fragilis* prefers pine stands (ČEIRĀNS 2002). Therefore, the discrepancy probably resulted from differences in Hylocomiosa canopy composition between both areas.

Among the drained forests, *A. fragilis* preferred pine, pine-spruce forests on mesoeutrophic soil, both on mineral soil and peat (Myrtillosa mel. and Myrtillosa turf. mel.). The herb layer in these forest types was similar to those of upland mesotrophic pine, pine-spruce forests (BUŠS 1997).

The species was totally absent in all wet forest types, raised bog and several drained types.

Zootoca vivipara habitat preferences

There was a significant positive correlation between the number of records and the transect length in a forest type for both study areas (KNP: R^2 = 45.2%, p = 0.002; GNP: R^2 = 79.1%, p = 0.002). However, forest type preferences were similar in both areas (table 2).

The species was present in most types of dry upland forests. However, the number of observations was lower than expected in most of the cases. The only exception (Vac-

Table 2: Transect length (TL) within forest types and deviations (D) from the expected proportion of records for reptiles in Ķemeri National Park (KNP) and Gauja National Park (GNP) in Latvia. Length of transects: no asterisk – less than 2 km; * – 2-5 km; ** - 5-10 km; *** - more than 10 km. NF – no reptile records on transect.

Tab. 2: Die Länge der Transekte (TL) in den Waldtypen und die Abweichung (D) vom erwarteten Wert der Reptiliennachweise in den lettischen Nationalparks von Ķemeri (KNP) und Gauja (GNP). Transektlänge: ohne Sternchen - weniger als 2 km; * - 2-5 km; ** - 5-10 km; *** - mehr als 10 km. NF – kein Reptiliennachweis auf dem Transekt.

Forest type /	TL (km)		*Anguis fragilis*		*Zootoca vivipara*		*Natrix natrix*
Waldtyp	KNP	GNP	KNP	GNP	KNP	GNP	KNP
Upland (dry) / auf höhergelegenen (trockenen) Böden							
Cladinoso-callunosa	11.2	1.1	NF***	NF	-0.58***	NF	NF***
Vacciniosa	9.8	1.7	0.35**	14.24	-0.52**	3.88	NF**
Myrtillosa	19.2	31.8	0.38***	0.22***	NF***	-0.28***	-0.21***
Hylocomiosa	18.2	46.3	1.90***	-0.16***	-0.22***	-0.15***	-0.16***
Oxalidosa	-	9.3	-	NF**	-	-0.55**	-
Aegopodiosa	-	2.3	-	NF*	-	NF*	-
Wet mineral soil / auf feuchten, mineralischen Böden							
Vaccinioso-sphagnosa	3.9	-	NF*	-	NF*	-	NF*
Myrtilloso-sphagnosa	13.4	0.6	NF***	NF	0.41***	2.49	1.34***
Myrtilloso-polytrichosa	1.5	-	NF	-	NF	-	NF
Dryopteriosa	2.9	-	NF*	-	NF*	-	1.64*
Wet peat soil / auf feuchten, torfigen Böden							
Raised bog / Hochmoor	16.1	5.6	NF***	NF**	1.64***	1.22**	-0.53***
Spagnosa, Caricoso-phragmitosa	29.4	2.8	NF***	NF*	0.45***	3.44*	-0.74***
Dryopterioso-caricosa	9.4	0.5	NF**	NF	NF**	NF	-0.19**
Drained / auf trockengelegten (entwässerten) Böden							
Callunosa turf. mel.	2.2	-	NF*	-	NF*	-	5.93*
Vacciniosa mel.	0.9	-	NF	-	NF	-	7.57
Vacciniosa turf. mel.	2.9	1.7	3.57*	NF	2.26*	0.22	6.90*
Myrtillosa mel.	11.1	-	3.76***	-	1.13***	-	-0.31***
Myrtillosa turf. mel.	18.3	-	0.44***	-	0.80***	-	-0.58***
Mercurialiosa mel.	13.3	-	NF***	-	-0.65***	-	-0.43***
Oxalidosa turf. mel.	14.4	-	-0.08***	-	NF***	-	1.65***

ciniosa type, GNP) should be considered as occasional because of short length of transect here.

Zootoca vivipara preferred several forest types from the group of wet forests. Typical habitats were stunted pine stands on raised bog that form a gradual transition to pine, pine-birch forests (Sphagnosa, Caricoso-phragmitosa) on wet *Sphagnum* and *Carex* peat, and also included partially drained areas (Vacciniosa turf. mel. type).

The species also showed preference for forests on moderately rich soils with mixed canopy composition and a *Vaccinium myrtillus* – dominated herb layer, in cases when they were not too wet nor completely dry. These were periodically wet (Myrtilloso-sphagnosa) or drained (Myrtillosa mel., Myrtillosa turf. mel.) forest types.

Zootoca vivipara was absent or found less than expected in all types of forests on rich soil where deciduous trees and spruce dominated the canopy.

Natrix natrix habitat preferences

The correlation between the number of *N. natrix* records and the transect length in forest types was not significant (KNP: $R^2 = 2.5\%$, $p = 0.53$).

The species was observed in a wide variety of forest types (table 2), being absent only in the driest pine forest types (Cladinoso-callunosa, Vacciniosa) and in two wet forest types (Vaccinioso-sphagnosam Myrtilloso-polytrichosa) with relatively small transect length.

Natrix natrix preferred periodically wet or drained forests, where it was typical for several types with mixed (pine-spruce-deciduous tree) canopy composition (Myrtilloso-sphagnosa) or with a spruce and deciduous tree canopy (Oxalidosa turf. mel.).

Table 3: Habitat niche breadth (NB) and Levin's niche breadth (NBLevins) for reptile forest habitats of Ķemeri National Park (KNP) and Gauja National Park (GNP), Latvia.

Tab. 3: Habitat-Nischenbreite (NB) und Levins Nischenbreite (NB_{Levins}) der Reptilienlebensräume in den Wäldern der lettischen Nationalparks von Ķemeri (KNP) und Gauja (GNP).

	KNP		GNP	
	NB	NB_{Levins}	NB	NB_{Levins}
Anguis fragilis	0.47	5.2	0.70	2.8
Zootoca vivipara	0.60	6.6	0.76	4.3
Natrix natrix	0.57	9.7	0.62	1.8

The species was also frequent in drained pine forests on poor *Sphagnum* and *Carex* peat (Callunosa turf. mel., Vacciniosa turf. mel.), around flooded peat mines in raised bogs. However, their pre-drained forest types (Sphagnosa, Caricoso-phragmitosa) and active raised bogs were avoided.

Habitat niche breadth and overlap

Habitat niche breadth index (NB) was higher than Levins's index (NB_{Levins}) in GNP and lower in KNP (table 3). However, the latter index may not be representative (see discussion). Two of the reptile species surveyed occupy wide habitat niches in forests: *Zootoca vivipara* can be regarded as the most generalized species among them, while *N. natrix* tends to inhabit moist forest. Data for the latter species in GNP may not be representative due to small number of observations there (n = 3). The third species - *A. fragilis* - prefers dry habitats (see above) that narrows its niche in wet areas such as KNP.

Niche overlap between the three most common forest reptile species was relatively high for both the percentage and Hurlbert's indexes (table 4). Remarkable was the high value of the latter index for *A. fragilis* with both, *Z. vivipara* and *N. natrix*, in KNP. An index value of > 1 indicates the trend of similar habitat use between two species, that in the case of the *A. fragilis* - *N. natrix* pair was unexpected. However, this result was mainly due to the overlap of habitats in the drained, not natural forests. In detail, 75% of the value of Hurlbert's niche overlap index in the *A. fragilis* – *N. natrix* pair, and 81% in the *A. fragilis* – *Z. vivipara* pair (and only 55% in the *Z. vivipara* – *N. natrix* pair) originated from the niche overlap in the drained forests, although they occupied only 32% of the transect length.

High niche overlap in the percentage index between *A. fragilis* and *Z. vivipara* in the Gauja National Park probably was associated with two factors: i) a large proportion of the dry forests (89 %) suitable for the former, and ii) wide use of various habitats (including dry forests) by the latter. The third forest species, *Natrix natrix*, is rare and unevenly distributed in this area.

DISCUSSION

Three reptile species (*A. fragilis*, *Z. vivipara*, *N. natrix*) were common in the surveyed forests. These species are the dominant reptiles also in the Białoweža Primeval Forest, where their records constituted 96% of all reptile observations (JĘDRZEJEWSKA & JĘDRZEJEWSKI 1998). The proportion of records for each reptile species in the Ķemeri National Park was similar to those of the Białoweža Forest (table 5). Therefore, the reptile communities in both can be considered as typical for northern nemoral – southern sub-boreal forests. In Gauja National Park one species (*N. natrix*) was rare, probably due to unfavorable climate conditions.

The observed distribution of *A. fragilis* within forest types can largely be explained by the moisture conditions as it avoids wet forests and raised bogs. The species was, however, observed in degraded bogs on sites with drained pine-birch forests (Vacciniosa turf. mel.) around old saturated peat mines. In contrast, the absence of *A. fragilis* in the driest forest type (Cladinoso-callunosa) can be explained by insufficient water supply in the habitat.

Another important factor is the preference of pine-dominated stands (ČEIRĀNS 2002a), over spruce or deciduous tree dominated forest types both upland (e.g., Oxalidosa) and drained (e.g., Mercurialiosa mel.).

Table 4: Indexes of reptile habitat niche overlap (percentage / Hurlbert's) in Ķemeri National Park (KNP; lower left of array) and Gauja National Park (GNP; upper right of array), Latvia.

Tab. 4: Die Überlappungsindizes der Reptilien-Habitatnischen (prozentuell / Hurlbert) in den lettischen Nationalparks von Ķemeri (KNP; unterer linker Teil der Matrix) und Gauja (GNP; oberer rechter Teil der Matrix).

	Anguis fragilis	*Zootoca vivipara*	*Natrix natrix*
Anguis fragilis	-	68 / 1.59 (GNP)	33 / 0.28 (GNP)
Zootoca vivipara	41 / 1.26 (KNP)	-	33 / 0.28 (GNP)
Natrix natrix	38 / 1.27 (KNP)	42 / 0.96 (KNP)	-

The only record of *A. fragilis* in drained spruce-deciduous forest (Oxalidosa turf. mel.) may be explained by migration from neighbouring pine stands.

The pattern observed in Latvia is verified by descriptions of the *A. fragilis* forest habitats in Lithuania (GRUODIS 1987) and Northern Belarus (PIKULIK et al. 1988). The herb layer described for *A. fragilis*-inhabited conifer plantations in the Netherlands (STUMPEL 1985) also is similar to that described for dry pine forest types in Latvia (BUŠS 1997).

Pine-dominated stands and young spruce stands are typical *Z. vivipara* habitats (ČEIRĀNS 2002a). The number of observations was less than expected in dry upland pine, pine-spruce forests. However, *Z. vivipara* records in these forests still formed a considerable part of all records in GNP (68.0 %), but not in KNP (9.5%). Data from present and previous studies suggest that in a sub-boreal forest *Z. vivipara* prefers habitats with considerable pine presence in the canopy (ČEIRĀNS 2002a), and with some extra soil moisture that persists even in drained stands.

As to *N. natrix* in the study area, the canopy composition is not correlated with the snake's distribution (ČEIRĀNS 2002a). The species has a great dispersal ability and a large home range (MADSEN 1984; SPELLERBERG 1988; ZUIDERWIJK et al. 1998), resulting in a wide habitat niche breadth.

In *N. natrix* clear preferences were observed for two drained forest types (Callunosa turf. mel., Vacciniosa turf. mel.) typical for the vicinity of old saturated peat mines. However, transect length in these types was insufficient for firm conclusions. Concerning forest types with transect lengths of more than 10 km, the *N. natrix* data showed positive preference values only for two more types (a wet and a drained type). In the study area these latter two types were also associated with a high density of amphibians (mainly *Rana temporaria* LINNAEUS, 1758) (pers. observ.), which are a main food resource for *N. natrix* (DROBENKOV 1995). Amphibian density (i.e. prey availability) is certainly among the factors determining the distribution of *N. natrix* in forest habitats. However, high amphibian density itself did not necessary result in the presence of *N. natrix* (pers. observ.).

Vipera berus (LINNAEUS, 1758), which was expected to be common in forests and bogs (see e.g., VIITANEN 1967; BELOVA 1976; GRUODIS 1987; OGNEV & LAPTIKOV 1989), was rarely encountered in both of the study

Table 5: Percentages of reptile species records in two National Parks of Latvia (present survey) and the Białoweža Primaeval Forest National Park of Poland and Belarus (JĘDRZEJEWSKA & JĘDRZEJEWSKI 1998).

Tab. 5: Der Prozentanteil der Beobachtungen von verschiedenen Kriechtierarten in zwei Nationalparks von Lettland (diese Untersuchung) und im Urwald-Nationalpark von Białoweža in Polen und Weißrußland (JĘDRZEJEWSKA & JĘDRZEJEWSKI 1998).

Species	Ķemeri National Park	Gauja National Park	Białoweža Primaeval Forest
Anguis fragilis	18	12	11
Lacerta agilis	2	2	1
Zootoca vivipara	49	79	52
Natrix natrix	30	5	33
Vipera berus	1	2	3
Total (%)	100	100	100

areas. This probably reflects regional differences in the distribution of the species, as *V. berus* is frequent in forests - at least in some areas of Latvia (pers. observ.).

Lacerta agilis LINNAEUS, 1758 was also a rare species in forest habitats in both study areas. Several records were made in dry pine forest types where *Calluna vulgaris*, *Vaccinium* species, and grasses are dominant in the herb layer. Stands with similar herb layer composition are typical for this species in temperate Western Europe (DENT & SPELLERBERG 1987; SPELLERBERG 1988; STUMPEL 1988; GLANDT 1991), although the canopy can be dominated by different conifer species. In other areas of sub-boreal Eastern Europe *L. agilis* also inhabits mainly dry pine (*Pinus sylvestris*) stands (GRUODIS 1987; PIKULIK et. al. 1988; VOITEHOV et al. 1989).

Use of Levins's index caused some counterproductive results when applied to the habitat niche surveys. In KNP, it produced higher values for *N. natrix* than for *Z. vivipara* although the observed distribution of the latter came closer to what was to be expected for species with wide niche breadth. In Levins's formula, maximum value of the niche breadth is attained when all habitat types are exploited at equal proportions. However, censuses were not carried out at equal proportions in all forest types. When Levins's formula was applied to the proportion of transects in the various forest types, it resulted in values of 7.5 in KNP and 3.3 in GNP (42% and 30% of the maximum, respectively). In two cases (*N. natrix* in KNP, and *Z. vivipara* in GNP) Levins's index for species was higher than this value. In both cases it simply indicated that the common forest types were not the most preferred. Another discrepancy was observed regarding differences between both National Parks. Index values were higher in KNP, although the coherence between the proportions of records and transect lengths was less marked than in GNP. Therefore, the application of Levins's index cannot be recommended for habitat surveys with unequal transect lengths in the various habitats.

Studies on the forestry impact on reptiles are relatively rare and deal mostly with the effect of tree logging in tropical forests (e.g., KUTT 1993; SARTORIUS et al. 1999; LIMA et al. 2001). The forestry impact in temperate Europe is largely overlooked. Some information has been collected during inventories and surveys on reptile ecology in clearings and young stands (e.g., BOSHANSKY & PISHCHELEV 1978; STUMPEL 1987; SPELLERBERG 1988). However, the effect of forest drainage on reptiles remains obscure.

In the present survey, reptile niches overlapped mostly in drained forests. These forests were favored by both dry forest species (*A. fragilis*) and species that prefer wet forest (*Z. vivipara*, *N. natrix*), which is possibly due to

i) intermediate moisture conditions; draining seldom is complete, and some extra moisture usually persists in the soil, making the habitat suitable for both dry and wet habitat species;

ii) stable water regime in the habitat due to drainage ditches; under natural conditions, in raised bogs and wet forests large areas can be homogeneously dry or wet depending on the season. This could have a negative effect on reptiles, especially on species with limited dispersal ability;

iii) impact of drainage ditches on habitat structure; the increase of habitat diversity due to the presence of suitable basking places, shrubs and grasses on the banks, and the presence of permanent water supply is essential for many animal species.

Of course, the conclusions drawn from a survey in one country cannot be extrapolated to the whole region of the temperate European forests. The study area (Latvia) is located in the middle of the sub-boreal forest zone (STANNERS & BOURDEAU 1994). Sub-boreal forests form a belt between boreal and nemoral forests, which gradually narrows from the Scandinavian Peninsula and Eastern Baltic to Western Siberia. Therefore, the present data can be regarded representative for the forests of the Baltic States, most of Belarus, and parts of Western Russia.

REFERENCES

AVIS, P. G. (1997): The forest typology in Latvia: an overview and comparison.- Proc. Latvian Acad. Sci. Section B, Riga; 51 (5/6): 195-199.

BELOVA, Z. V. (1976): Spatial structure of a population of the adder (*Vipera berus* L.).- Ekologija (Russian J. ecol.), Moscow; 7 (1): 71-75. [In Russian].

BOSHANSKY, A. T. & PISHCHELEV, V. A. (1978): Effect of some forms of economical activity on distribution and numbers of *Vipera berus*.- Zoologicheskij Zhurnal., Moscow; 57 (11): 1695-1698. [In Russian with English abstract].

BUŠS, K. (1997): Forest ecosystem classification in Latvia.- Proc. Latvian Acad. Sci. Section B, Riga; 51 (5/6): 204-217.

ČEIRĀNS, A. (2002a): On the importance of tree stand composition and age in forest habitats of *Anguis fragilis, Zootoca vivipara*, and *Natrix natrix*.- Herpetozoa, Wien; 15 (1/2): 63-74.

ČEIRĀNS, A. (2002b): Reptiles and amphibians of the Gauja National Park, Latvia.- Biota, Radoživ; 3 (1/2): 17-25.

DENT, S. & SPELLREBERG, I. F. (1987): Habitats of the lizards *Lacerta agilis* and *Lacerta vivipara* on forest ride verges in Britain.- Biol. Conserv., London; 42: 273-286.

DROBENKOV, S. M. (1995): Comparative analysis of diet in sympatric snakes *Vipera berus* (L.), *Natrix natrix* (L.), *Coronella ausriaca* (LAUR.).- Ekologija, (Russian J. ecol.), Moscow; 26 (3): 222-226. [In Russian].

GLANDT, D. (1991): The vegetation structure preferred by the sand lizard (*Lacerta agilis*) and the common lizard (*Lacerta vivipara*) in an experimental outdoor enclosure.- Acta Biol. Benrodis, Düsseldorf; 3: 79-86.

GREENBERG, C. H. (2001): Response of reptile and amphibian communities to canopy gaps created by wind disturbance in the Southern Appalachians.- Forest Ecol. Managem., Amsterdam (Elsevier); 148: 135-144.

GRUODIS, S. (1987): Amphibians and reptiles; pp. 144-149. In: SOKOLV, V. J. (Ed.): Ecological optimization of agrolandscape; Moscow (Nauka Publ.). [In Russian with English summary].

JĘDRZEJEWSKA, B. & JĘDRZEJEWSKI, W. (1998): Predation in vertebrate communities: the Białoweża Primeval Forest as a case study; Berlin, Heidelberg (Springer-Verlag); 450 pp.

KABUCIS, I. (Ed.) (2000): Handbook of habitats. Protected habitats by European Union in Latvia; Riga (Latvijas Dabas Fonds); 160 pp. [In Latvian].

KAVACS, G. (Ed.) (1995): The encyclopedia of Latvia's nature; Vol. 2; Riga (Latvijas enciklopēdija). [In Latvian]; 256 pp.

KAVACS, G. (Ed.) (1998): The encyclopedia of Latvia's nature; Vol. 5; Riga (Latvijas enciklopēdija); 255 pp. [In Latvian].

KREBS, C. J. (1989): Ecological methodology; New York (Harper & Row Publishers); pp. 654.

KUTT, A. (1993): Initial observations on the effect of thinning eucalypt regrowth on heliothermic skinks in lowland forest, East Gippsland Victoria; pp. 187-196. In: LUNNEY, D. & AYERS, D. (Eds.): Herpetology in Australia – a diverse discipline. Sydney (Royal Zoological Society of New South Wales).

LIMA, A. P. & SUAREZ, F. J. & HIGUCHI, N. (2001): The effects of selective logging on the lizards *Kentropyx calcarata, Ameiva ameiva* and *Mabuya nigropunctata*.- Amphibia-Reptilia, Leiden; 22: 209-216.

MADSEN, T. (1984): Movements, home range size and habitat use of radio-tracked grass snakes (*Natrix natrix*) in Southern Sweden.- Copeia, Lawrence; 1984 (3): 707-713.

OGNEV, A. V. & LAPTIKOV, J. M. (1989): Distribution and some ecological features in the adder, *Vipera berus*, in the Moscow District; pp. 37-39. In: JANSHIN, A. (Ed.): Amphibians and reptiles of the Moscow District; Moscow (Nauka Publishers). [In Russian].

PIKULIK, M. M. & BAHAREV, V. S. & KOSOV, S. V. (1988): Reptiles of Belarus; Minsk (Nauka i Tehnika Publishers), 166 pp. [In Russian].

PRIEDĪTIS, N. 1999: Latvian forest – nature and diversity; Riga (WWF), 209 pp.

SARTORIUS, S. S. & VITT, L. J. & COLLI, G. R. (1999): Use of naturally and anthropogenically disturbed habitats in Amazonian rainforest by the teiid lizard *Ameiva ameiva*.- Biol. Conserv., London; 90: 91-101.

SPELLERBERG, I. F. (1988): Ecology and management of reptile populations in forests.- Quarterly J. Forestry, Ashford; 82: 99-109.

STANNERS, D. & BOURDEAU, P. (1995): Europe's Environment: The Dobris Assessment. Luxembourg (Office for official publications of the European communities), 676 pp.

STUMPEL, A. H. P. (1985): Biometrical and ecological data from a Netherlands population of *Anguis fragilis* (Reptilia, Sauria, Anguidae).- Amphibia-Reptilia, Leiden; 6: 181-194.

STUMPEL, A. H. (1988): Habitat selection and management of the sand lizard *Lacerta agilis* L., at the Utrechtse Heuverlug, Central Netherlands.- Mertensiella, Rheinbach; 1: 122-131.

VIITANEN, P. (1967): Hibernation and seasonal movements of the viper, *Vipera berus berus* (L.), in Southern Finland.- Ann. zool. Soc. Zool. Bot. Fennicae Vanamo, Helsingfors; 4 (4): 472-546.

VOITEHOV, M. J. & LESHCHEVA, T .S. & FLINT, V. E. & FORMOZOV, N. A & GARUSHJANC, K. J. (1989): Short notes on amphibian and reptile fauna of the Moscow City and the Moscow District; pp. 43-48. In: JANSHIN, A. (Ed.): Amphibians and reptiles of the Moscow District; Moscow (Nauka Publishers). [In Russian].

ZUIDERWIJK, A. & DE WIJER, P. & JANSSEN, I. (1998): The decline of a grass snake metapopulation near Amsterdam; pp. 463-470. In: MIAUD, C. & GUYETANT, R. (Eds.): Studies in herpetology; Le Bourget du Lac (Societas Europaea herpetologica).

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