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Habitat ecology of the smooth snake *Coronella austriaca* and its reptilian prey in the degraded bog with implications for artificial refuge surveys

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ABSTRACT

Diet preferences of the smooth snake (*Coronella austriaca*) being still controversial, we studied the overlap between its habitat and that of its potential reptilian prey species using the artificial refuge (ATR) method. The discriminant function analysis revealed that part of the smooth snake's habitat niche is unused by one of its prey species – *Zootoca vivipara*. The smooth snake was recorded more often in places with high density of individuals of another lizard species – *Anguis fragilis*. Occasional data on snake diets supported the assumption that the latter species is a very important food item for the smooth snake in the study area. Our study estimated the minimum number of times that a site must be visited to infer absence of a particular species, which was 12 for *Anguis fragilis*, 14 for *Coronella austriaca*, and 19 for *Natrix natrix*. Moreover, the study revealed that ATRs should be placed and kept at a site for the whole vegetation season. In the intact bog habitat, the smooth snake was recorded only within a 40 m wide peripheral belt, *Anguis fragilis* within an 80 m wide belt, and *Zootoca vivipara* within a 120 m wide peripheral belt. In the drained bog, *Anguis fragilis* inhabited a broad spectrum of habitat types ranging from tall closed forest to low open stands. All other species inhabited stands with the tree cover percentage smaller than 30–50%. *Coronella austriaca* and *Vipera berus* preferred low stands (average height < 5 m), while *Zootoca vivipara* and *Natrix* did not show any preferences for tree stand height. Our study indicates that reptiles benefit from lowered ground water levels and more stable water regime of a degraded bog.

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Introduction

The smooth snake (*Coronella austriaca*) is a relatively small, secretive snake included in the European Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora (or 'Habitat Directive') Annex IV and evaluated as being in an unfavorable state in all countries of Central and Northern Europe (European Topic Center on Biological Diversity Database, http://bd.eionet.europa.eu).

Throughout the range, it inhabits various semi-open habitats such as forest edges, clearings, stony habitats, abandoned anthropogenic sites (Luiselli, Capula, and Shine 1996; Drobenkov 2000; Kery 2002; Najbar 2006; Santos et al. 2009). Of particular importance in some parts of the range are habitats with a dense heath cover, such as open lowland heaths of Northwest-Southern England (Pernetta 2009; Reading 2012) and the Netherlands (Stumpel and van der Werf 2012), or drained peat bogs of northeast Latvia (Čeirāns 2000). Bogs are habitats of particular conservation interest due their role as carbon sinks (Belyea and Malmer 2004; Vanselow-Algan et al. 2015).

There is some controversy regarding feeding habits of the smooth snake. Studies conducted in Great Britain indicate a large proportion of mammalian prey constituting 28–45% of their diets (Reading and Jofre 2013; Brown, Ebenezer, and Symondson 2014) with nesting mammalian prey sometimes suggested as the most important dietary item here (Goddard 1984). Studies carried out in continental parts of the range – Belarus (Drobenkov 2000) and Italy (Luiselli, Capula, and Shine 1996) indicated an insignificant proportion of mammals in snake diets (5–7%). The study of the smooth snake population in Latvia showed that population densities of lacertid lizards, which were the most important food item in all the diet studies mentioned above, were low or they were absent from some snake sub-populations in degraded raised bogs (Čeirāns and Nikolajeva 2014). In captivity, most of the snakes that originated from this population have refused mammalian prey, and consumed only reptiles (Čeirāns 2000). Hence, this population should have other reptile species as important food items. During the reptile habitat study which was conducted here in 2010–2014 using artificial refuges (ATRs), it turned out

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that it is very difficult to collect significant snake diet data, because keeping snakes in captivity for the purpose of collecting their feces was not possible, and only in two cases we managed to force snakes to regurgitate their food. In one case the regurgitated food item was a large slow worm (*Anguis fragilis*), but in another – an adult viviparous lizard (*Zootoca vivipara*). Therefore here we explore the relative importance of snake feeding items indirectly by evaluating the co-presence of snakes and other reptiles and by evaluating their habitat niches.

Reptiles can use various natural and artificial covers as hiding places under which they can be easily counted. The ATR method (Reading 1997) is particularly suitable for sites with a dense ground cover and for such species as the smooth snake (*Coronella austriaca*) and the slow worm (*Anguis fragilis*), which are seldom seen on the open ground. ATRs can be made of different materials, for example onduline bitumen sheets (Thierry et al. 2009; Lettink, O'Donnell, and Hoare 2011) or plywood (Mutz and Glandt 2004), but in Europe most often used are dark colored profiled iron plates (Pernetta 2009; Stumpel and van der Werf 2012; Čeirāns and Nikolajeva 2014; Reading and Jofre 2015). The use of iron ATRs in snake studies produces better results than ATRs made of plywood, but both materials are equally effective for investigating other species (Mutz and Glandt 2004). It is suggested that iron ATRs are used not only for shelter, but also for thermoregulation (Mutz and Glandt 2004; Thierry et al. 2009). Consequently, ATR use should vary depending on the weather, temperature and, probably, there are some daily and seasonal use patterns. The data available on the number of visits necessary for the detection of reptile species are scarce. Estimations of the number of site visits for various species vary from 4–34 during visual encounters (Kery 2002) to 1–5 visits using the ATR method (Sewell et al. 2012).

The aim of the present study was to ascertain whether snakes share sites with all other reptiles, whether the habitat niche of the potential reptilian prey completely covers that of the snake, or whether there are cases when some part of the habitat can be unused by a prey species. An additional task was to identify the duration of iron ATR placement in a habitat and the number of their checks necessary for obtaining reliable data, and to study whether there are particular air temperature, seasonal or daily patterns in ATR use by reptiles.

Materials and methods

Site description

The present study was conducted in the Ķemeri National Park, which is located in the central part of Latvia, south of the Riga Gulf, some 25 km west of the Riga City. The survey site is located in the north-eastern part of the National Park, in the Slokas un Vecais Bog. The total area of the bog is more than 650 ha. It is strongly altered by old peat pits presently filled with water, which cover about 1/4 of the bog area. The change in water level and bog drainage have caused the overgrowth of peripheral parts of the bog with pine and birch forest, with most of the remaining open area turning into degraded raised bog habitat with only a minor part of it retaining its relatively natural state. The map of the area with a more detailed location of the study site and placement of ATR groups is published elsewhere (Čeirāns and Nikolajeva 2014).

Data collection

The data were collected in 2011–2014 by placing ATRs-profiled, dark brown tin plates with dimensions of 1.0 × 0.5 m – in the habitat. ATRs were placed randomly at a distance of 6–30 m from one another at 18 sites (not all of them were sampled in the same year), in groups of 5–35 ATRS (average – 15). They covered all the range of bog microhabitats. Obviously unfavorable habitats, such as dense tall forest stands, were intentionally undersampled with only a few ATRs placed there for reference. ATRs were not placed directly on a 3–5 m wide roadside vegetation belt because of the high risk of ATR theft or vandalism. A total of 100 ATRs were placed in 2011, 103 in 2012, 49 in 2013, and 120 in 2014. Fifteen percent of ATRs were placed in the same place as in the previous year, but the rest of them – in new places. ATRs were placed in May or June and removed in September. The first checking of ATRs was done about one week after their placement. Further visits were made twice a week in dry weather conditions; in the case of rain onset and sharp drop of temperature surveys were terminated. The number of visits varied from 19 to 27 (average 22) depending on the year and the ATR group. During a visit, air temperature at a height of 1.5 m, weather conditions (sunny, cloudy etc.) and time of the survey beginning and end were recorded for each site. A total of 215 sightings of *Coronella austriaca*, 717 of *Anguis fragilis*, 77 of *Zootoca vivipara*, 42 of *Natrix natrix*, 35 of *Vipera berus* were recorded under ATRs. *Coronella austriaca* was found under 23%, *Anguis fragilis* – 56%, *Zootoca vivipara* – 21%, *Natrix natrix* – 9%, but *Vipera berus* – 4% of all ATRs.

To evaluate the extent of ATR use, freely moving reptiles were also recorded; 95% of *Coronella austriaca*, and 93% of *Anguis fragilis* records were under ATRs, additional 1.5% and 5% of records respectively were dead animals on seldom used dirt roads. *Vipera berus* accounted for 78%, *Zootoca vivipara* for 60%, and *Natrix natrix* for 38% of all the records under ATRs.

Vegetation was described in a circular plot, the center of which coincided with that of an ATR. Vegetation data were described as vegetation coverage percentage, which was evaluated visually to the nearest 1, 5, 10, 20, 30, 40 etc. %. It was estimated separately for taxa at a species or genus level, and following vegetation height storeys: 0–0.20, 0.21–0.50, 0.51–0.99, 1.00–9.99, ≥10 m. The plot radius was 1.5 m, with the exception of higher vegetation storeys – 5.0 m for 1.00–9.99 m, and 10.0 m for ≥10 m high vegetation.

Data analyzes

Our data showed positive relationships between species densities and search efforts made (days or ATR checks) until the first specimen was recorded. It allowed us to use Poisson regression to build models instead of using probabilities of records and arbitrary population density divisions into three groups – low, medium, and high (Kery 2002) or their complete absence (Sewell et al. 2012). Instead of categorized data we had continuous data sets with three selected reference values – minimum (function values at zero), maximum (function values at maximum observed in nature) and median (function values in the middle between zero and maximum observed in nature). The number of ATRs at a site was not an important factor, because in all species, correlations between the number of ATRs and the number of site visits until the first specimen record had $p > 0.1$. For site models we used only the cases (site-years) with at least 20 visits, 10 ATRs, and a full season of ATR placement. Two models for each species were used: (i) for the whole site and (ii) for an individual ATR.

To determine seasonal and daily patterns in ATR use by reptiles, their use (the average number of individuals per visit) was plotted against the date, temperature, daytime, and solar conditions. Generalized linear models (GLM) and generalized additive models (GAM) were used to test significance of these relationships. To remove the effect of great variation in species densities among sites and years, the data on ATR use were divided by the maximal value for a given species at a given site that year. The date and daytime were transformed into the decimal system. The daytime was calculated as the middle between the start and end of ATR checks at a given site (usually 0.5–1.5 h long). Solar conditions were categorized as follows: 1 – overcast; 2 – variable overcast and sunny weather; 3 – sunny weather. XY (Z) plots were used to visualize relationships among the pooled data on 10 ATRs (216 observations) in which at least 3 individuals of the most often recorded species – *Anguis fragilis*, were found simultaneously at least once.

To determine whether a potential prey species avoids sharing shelters with *Coronella austriaca* or not, we used comparisons of reptile average densities per check between ATRs with and without *Coronella austriaca* ($n = 37$ and 189 respectively). However, it is possible that *Coronella austriaca* prefers areas with higher densities of prey species, although prey avoids particular shelters that are at that moment occupied by the snake. To test this assumption, we compared average densities of reptile species under plates with and without *Coronella austriaca* within a 30 m radius. Only cases with 3 or more ATRs available within a 30 m radius were analyzed ($n = 35$ and 109 for ATR with and without a snake respectively). The Mann-Whitney W test for statistical significance and Box plots for data visualization were used.

The discriminant function analysis (DFA) was performed to compare the habitat niche of *Coronella austriaca* and two potential prey species – *Anguis fragilis* and *Zootoca vivipara*. Vegetation descriptions of 44, 121 and 38 plots respectively were used. The majority of correlations between vegetation variables were well below 0.50, and all were included in the analysis.

Wooded vegetation in the study area was single-storey, without significant shrub or young tree understorey. XY (Z) plots were used to examine the combined effect of the tree storey average height and coverage on the frequency of snake records under ATRs. Such plots allowed identifying thresholds and relationships that did not show statistically significant functions.

One particular site was chosen for the study of forest and roadside edge effects. It was a place where a gravel road with a distinct 3 m wide roadside vegetation belt went perpendicularly to a wet intact bog and the edge of drained tall forest. Here, the forest edge showed a dramatic change in vegetation with complete transition of ground vegetation form one type to another within just a 10–15 m wide belt. Owing to its southern exposition, the forest edge was particularly suitable for reptiles. There were 51 bog and 12 forest ATRs at this location, and their distance from the forest edge and roadside was measured at the site or from Google Earth maps using GPS coordinates. XY (Z) plots were used to visualize the location of reptile record in relation to the distance from the road and the forest edge.

All statistical analyzes and all charts were performed using SPSS PASW Statistics 18, Statgraphics Plus 5.0, and CANOCO for Windows 4.5 software.

Results

The minimum number of necessary sampling days and visits

In the case of three reptile species, the site data showed a statistically significant relationship between the number of ATR checks until the first specimen record and their relative density (Table 1).The *Anguis fragilis* model ($p < 0.0001$) indicated that the minimum number of visits necessary for species detection or absence confirmation with 95% confidence was 12, while for *Coronella austriaca* ($p < 0.0001$) this number was – 14. At maximum population density, these models indicated that 2 visits are sufficient for *Anguis fragilis*, and 4 visits for *Coronella austriaca*. The model for *Natrix natrix* was weak but significant ($p = 0.003$) with great dispersion of observation data. This model suggested that a considerably larger number of visits was necessary for the detection of a minimum density population (19 visits),

Table 1. Poison regression statistics for the relationship between the relative species density (independent variable) and site visits until the first species record at an ATR site (95% confidence limits in parentheses; p for N. natrix = 0.003, for other cases p < 0.0001).

Species	*N*	Argument at independent variable	χ^2	Adjusted explained deviance (%)	Visits at minimum density	Visits at medium density	Visits at high density
Coronella austriaca	22	−0.189	28.2	26.1	10.5 (13.7–7.9)	4.3 (5.9–3.8)	1.6 (3.8–0.9)
Anguis fragilis	25	−0.110	36.7	35.3	8.7 (12.1–6.1)	3.0 (4.0–2.4)	1.1 (2.1–0.9)
Natrix natrix	10	−0.222	9.63	6.36	14.4 (19.2–10.6)	6.0 (11.8–3.5)	2.3 (4.2–0.7)

Table 2. Poison regression statistics for the relationship between the average reptile observation frequency under individual ATRs (independent variable) and the number of its checks until the first record (95% confidence limits in parentheses; p for V. berus = 0.02, for all other cases < 0.0001).

Species	*N*	Argument at independent variable	χ^2	Adjusted explained deviance (%)	Checks at minimum density	Checks at medium density	Checks at high density
Coronella austriaca	37	−0.045	55.8	37.3	20.0 (23.3–17.3)	8.2 (10.1–7.0)	3.1 (4.9–2.1)
Anguis fragilis	122	−0.032	129.0	20.9	12.5 (13.9–11.3)	3.8 (4.6–3.1)	1.0 (1.4–0.8)
Zootoca vivipara	46	−0.087	27.4	13.5	20.0 (24.0–16.0)	7.1 (9.2–6.0)	2.4 (5.0–1.1)
Natrix natrix	22	−0.059	11.6	6.0	22.4 (28.9–17.6)	14.4 (16.3–12.8)	9.2 (12.9–6.8)
Vipera berus	9	−0.044	15.15	35.5	20.0 (26.3–15.9)	8.5 (11.2–7.0)	4.4 (9.1–1.7)

Table 3. Poison regression statistics for the relationship between the average reptile observation frequency under individual ATRs (independent variable) and days until the first record (95% confidence limits in parentheses; p in all cases < 0.0001).

Species	*N*	Argument at independent variable	χ^2	Adjusted explained deviance (%)	Days at minimum density	Days at medium density	Days at high density
Coronella austriaca	37	−0.047	323.2	40.3	112 (119–105)	44 (48–39)	18 (20–16)
Anguis fragilis	122	−0.020	307.0	11.5	58 (60–56)	28 (30–26)	11 (13–10)
Zootoca vivipara	46	−0.058	73.7	8.6	88 (96–79)	45 (49–41)	21 (29–17)
Natrix natrix	22	−0.051	39.7	7.0	94 (106–84)	63 (66–61)	43 (50–37)
Vipera berus	9	−0.038	65.3	41.1	102 (116–89)	46 (53–40)	21 (29–16)

but for maximum density populations, values (4 visits) were similar to those regarding another snake species – *Coronella austriaca*.

Models for the number of checks of individual ATRs were statistically significant for all the species under study ($p < 0.0001$) with a marginally significant relationship recorded only for *Vipera berus* ($p = 0.02$) (Table 2). They predictably indicated a larger number of necessary checks compared with site models. All models for the number of days required until the first record were statistically significant ($p < 0.0001$), indicating that actually the whole field season was necessary to confirm the presence or absence of a species (Table 3). *Anguis fragilis*, whose model indicated that just 2 months are sufficient to confirm the presence or absence of the species at minimal densities, was the only exception. However, this model explained a relatively small percentage of variation in observations, and observation data had very large dispersion. Thus, in some cases, when species density was low, actual numbers of days until first records were 2.2 times, and numbers of ATR checks 1.8 times larger than predicted by the model.

All data sets on *Zootoca vivipara* and *Natrix natrix* had very large dispersions, and models explained a relatively small part (6–14%) of variation. The first record of maximum density *Natrix natrix* populations required a considerably larger number of checks and days compared with that of other species, which may indicate a lower use of ATRs by reptiles of this species. Conversely, models for *Coronella austriaca* and *Vipera berus* were similar and explained 35–41% of variation, which may indicate a better use of ATRs by these species.

Patterns in ATR use

There were very few significant relationships determined between reptile record frequency and date, time or air temperature. *Vipera berus* was recorded more often in July and August (GAM, $n = 20$, $F = 5.53$, $p = 0.005$), but the sample size was small ($n = 20$). *Zootoca vivipara* was found more often under ATRs on overcast days or in variable weather conditions than in full sun (GLM, $n = 49$, $F = 8.61$, $p = 0.004$).

XY (Z) plots for the pool of data on ten ATRs most extensively used by *Anguis fragilis* showed that this species was recorded here at a rather distinct thermal interval, which was the same at different time of the day and in different months (Figure 1). There were no clear daily or seasonal patterns revealed, however. Optimal count results were obtained at the air temperature ranging from19 to 22 °C, but its drop below 16 °C caused the abandonment of ATRs by reptiles. For comparison, minimum temperatures for *Coronella austriaca* in autumn were considerably lower – 12 °C in sunny, and 13 °C in overcast weather.

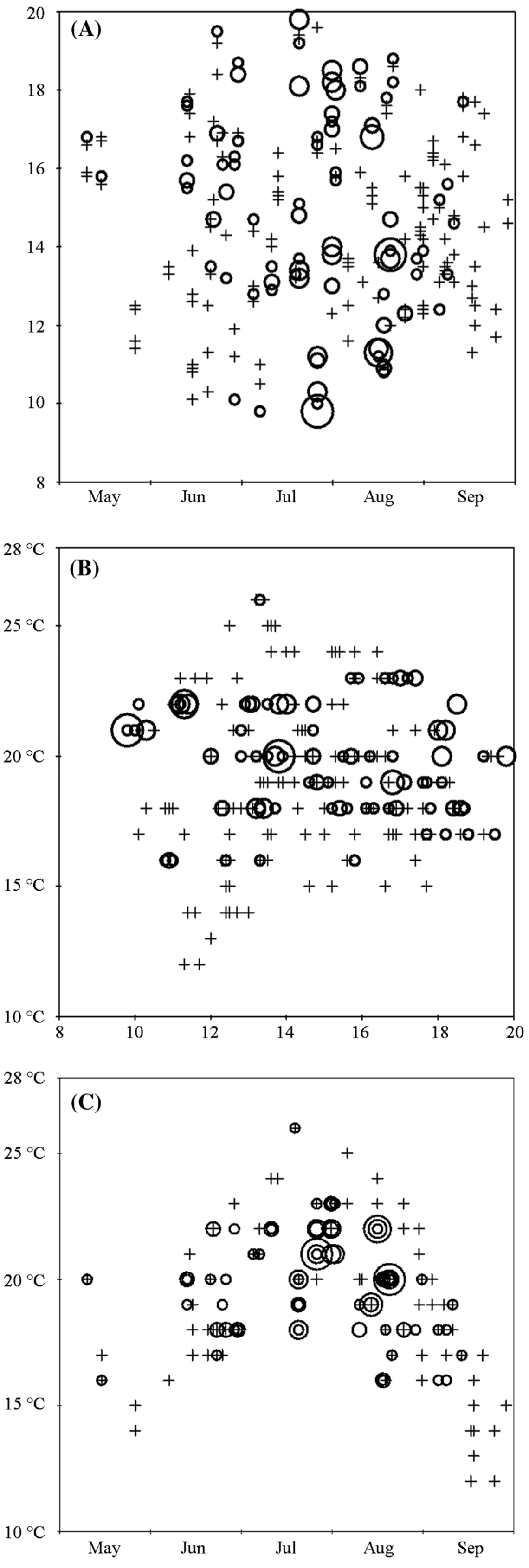

Figure 1. Temperature, daytime and date relationships to the number of observed *Anguis fragilis* individuals under ten most used ATRs; the size of a circle corresponds to the number of individuals (from 1 to 6); crosses indicate cases when the species was absent.

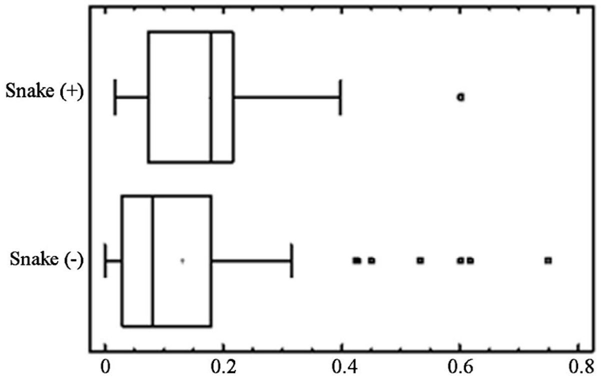

Figure 2. Average records of *Anguis fragilis* within a 30 m radius from ATRs with (top) and without (bottom) *Coronella austriaca* ($p < 0.01$).

Co-presence of Coronella austriaca *with reptilian prey species*

This study did not find avoidance by any reptile species of the ATRs used by *Coronella austriaca* ($p > 0.1$ in all cases). However, we ascertained that the number of *Anguis fragilis* individuals in the ATRs inhabited by *Coronella austriaca* within a 30 m radius was greater compared with that in uninhabited ATRs ($p < 0.01$; Figure 2). There were no correlations found with densities of other reptile species.

Microhabitat overlap among species

Coronella austriaca microhabitats in the Slokas Bog are characterized by low vegetation taxonomic diversity represented by species typical of more or less degraded oligotrophic raised bog habitat. Vegetation characteristics of *Coronella* microhabitats are described in detail elsewhere (Čeirāns and Nikolajeva 2014).

In DFA analysis, the first two discriminant functions (DF) correctly classified 40.4% of original cases, explained 58 and 42% of variance respectively, but both had low eigenvalues (0.038 and 0.028 respectively) at statistical significance $p < 0.05$. However, when considering correlations in the DFA structure matrix (Table 4), both functions had a sound biological explanation. DF1 showed the drainage gradient from taxa and characters of tall forest stands developed on drained soils of a former bog (represented by ≥10.0 m vegetation, forest species *Vaccinium myrtillus*, *Vaccinium vittis-idaea*, *Empetrum nigrum*, non-*Sphagnum* mosses, bare ground) to those of an unaltered, wet, open bog (dense, lowest storey vegetation, *Calluna vulgaris,* medium wooded vegetation with *Pinus sylvestris*). DF2 showed the trophic gradient from oligotrophic bog habitat (represented by *Sphagnum* mosses, *Calluna vulgaris*) to ruderal lush vegetation on enriched soils (represented by *Aegopodium podagraria*, *Urtica dioica*, *Trifolium* sp.) of strongly altered habitats (eg embankments, dumps).

In the DFA chart, the microhabitat range of *Coronella austriaca* completely overlapped with that of *Anguis fragilis*, but not with that of *Zootoca vivipara* (Figure 3). The chart showed a notable sector at high values of DF2, where the former two species were present, but the latter was absent. Group centroid values at DF2 were identical for *Coronella austriaca* and *Anguis fragilis* (0.08), but considerably lower for *Zootoca vivipara* (–0.35).

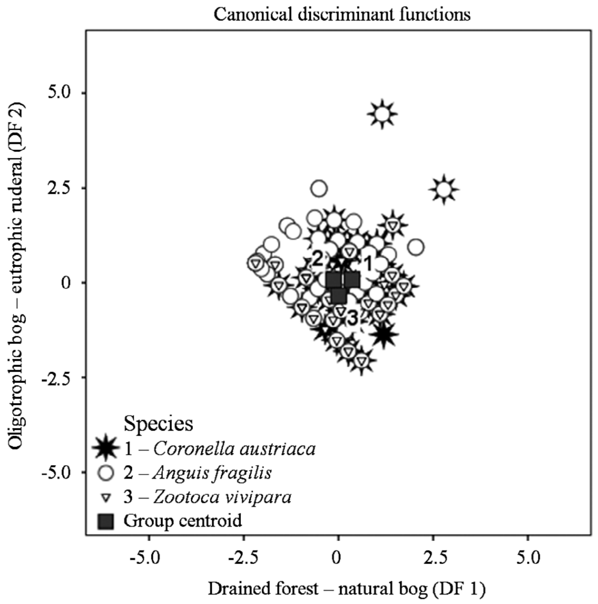

Figure 3. Discriminant function analysis (DFA) chart for the differentiation among *Coronella austriaca*, *Anguis fragilis*, and *Zootoca vivipara* microhabitat niches.

Table 4. DFA structure matrix; only variables with correlations more than 0.1 with at least one discriminant function (DF) are shown.

Variable	DF 1	DF 2
Pinus sylvestris	0.32	–0.35
Picea abies	–0.09	0.10
Betula sp.	–0.01	0.16
Calluna vulgaris	0.76	–0.65
Vaccinium myrtillus	–0.42	0.18
Vaccinium vitis-idaea	–0.32	0.22
Empetrum nigrum	–0.33	0.09
Andromeda polifolia	–0.05	–0.11
Urtica dioica	0.02	0.45
Aegopodium podagraria	0.05	0.45
Oxalis acetosella	–0.15	0.03
Trifolium sp.	0.04	0.47
Melampyrum pratense	–0.13	0.17
Eriophorum vaginatum	–0.03	–0.12
Calamagrostis sp.	–0.08	0.21
Scirpus sylvaticus	–0.06	0.20
Molinia caerulea	–0.08	0.13
Pteridium aquilinum	–0.09	0.10
Equisetum sp.	0.11	0.44
Sphagnum mosses	0.11	–0.31
Non-*Sphagnum* mosses	–0.38	0.10
Bare ground	–0.29	0.34
0.21–0.50 m vegetation	0.46	–0.39
0.51–0.99 m vegetation	–0.04	0.22
1.00–9.99 m vegetation	0.70	0.73
≥10.0 m vegetation	–0.62	0.07

Tree storey effect

At the study site, the taxonomic composition of tree stands was highly uniform: they were dominated by pine (*Pinus sylvestris*) (in the whole set of sampling plots canopy coverage 5–90%, average – 23 ± 12.8, median – 20) with birch (*Betula pubescens*, *B. pendula*) admixture (coverage 0–40%, average – 8 ± 8.8, median – 5), the presence of other wooded vegetation – spruce (*Picea abies*), willow (*Salix* sp.) being insignificant. There were no statistically significant correlations found between tree species proportions and reptile records (GLM, $p < 0.1$). However, XY (Z) plots showed that *Coronella austriaca* was most often recorded in low stands with the average height below 4 m, and 20–30% canopy coverage (Figure 4). In sparser or taller stands, it was found less often, and from stands with the average height above 13 m, or with 40% canopy cover, it was usually absent. By contrast, *Anguis fragilis* occupied the whole range of surveyed stands including tall forest. Another potential prey species – *Zootoca vivipara*, also occupied a wider range than *Coronella austriaca*, with the tree cover being a single important factor. It was absent from stands with the canopy cover over 40%. *Natrix natrix* was absent from closed forest (tall stands with high canopy cover percentages), and did not show any tree stand preferences other than 50% or less canopy closure. During the study, *Vipera berus* was observed only in stands with the average height lower than 8 m (most often < 5 m) and tree cover up to 40%.

Forest and roadside edge effects

Only three reptile species were found at the site used for edge effect exploration. They differed in their ability to use intact bog and drained forest habitat (Figure 5). *Coronella austriaca* inhabited about 35 m wide peripheral belts of the raised bog, both at the roadside and forest edge, and sometimes occurred about 30 m deep in the tall closed forest. *Anguis fragilis* fully exploited forests developed on drained parts of a former bog, but was absent from sites in the intact raised bog that were farther than 80 m. On the contrary, *Zootoca vivipara* was found only up to 40 m deep in the forest, but in the bog it was present far behind its edge vegetation belt at least 120 m deep in the intact habitat.

Discussion

Implications for ATR surveys

Our results do not confirm some published estimations where 95% confidence models indicated that in ATR surveys only 1–2 visits were necessary for the detection of *Anguis fragilis*, 2–3 visits for that of *Coronella austriaca* and *Zootoca vivipara*, and 3–5 for the detection of *Natrix natrix* and *Vipera berus* (Sewell et al. 2012). Our

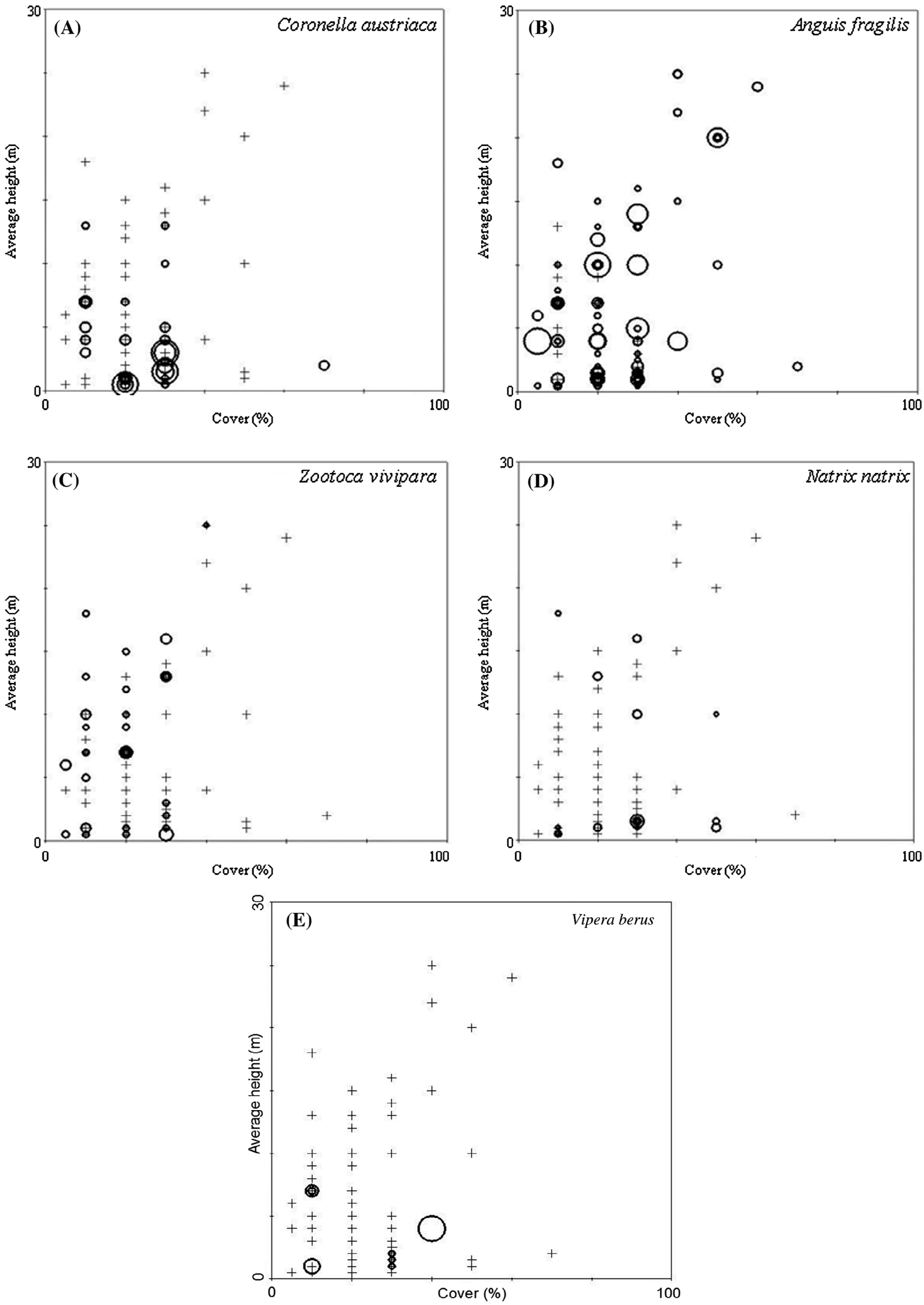

Figure 4. The relationship of the tree storey cover and average height with reptile records; the size of a circle corresponds to the ATR use frequency (average number of individuals per one check), which in *Coronella austriaca* is in the range 0.02–0.40, in *Anguis fragilis* – in the range 0.02–1.00, in *Zootoca vivipara* – in the range 0.02–0.14, in *Natrix natrix* ranges between 0.02 and 0.19, and in *Vipera berus* between 0.02 and 0.32; crosses indicate cases when the species was absent.

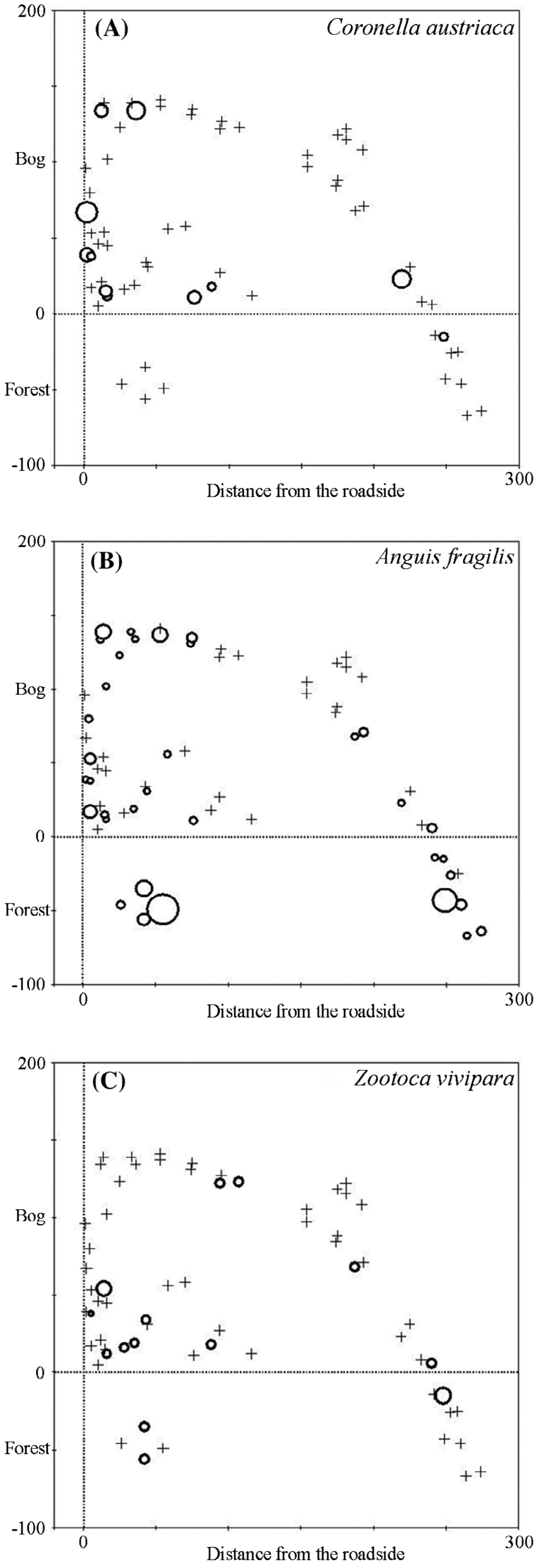

Figure 5. Distances (m) from the roadside (*x* axis) and the raised bog-forest edge (*y* axis) to reptile recording locations; the size of a circle corresponds to the ATR use frequency (average number of individuals per one check), which at this site varied between 0.02 and 0.17 in *Coronella austriaca*, between 0.02 and 0.95 in *Anguis fragilis*, and between 0.02 and 0.10 in *Zootoca vivipara*; the forest edge at the sampling site is with a southern exposition.

data showed that such a number of visits would be sufficient only for the detection of maximum density populations. To estimate sampling efforts needed for species detection when population size is not known, the population should be assumed to be small and low density one. Our research shows that it is not possible to reduce the study period to just a few weeks of ATR survey or to several visits. Models for sites indicated that in the case of the smooth snake (*Coronella austriaca*), ATRs should be checked at least 14 times in order to assume (based on 95% probability) that this site is unoccupied. It is still considerably less than 32–34 visits necessary for the detection of a small smooth snake population by conducting less efficient visual searches (Kery 2002; Hartel et al. 2009). Our model for the slow worm (*Anguis fragilis*), a species that is most often recorded under ATRs, showed that at least 12 ATR checks were necessary to infer species absence. The model for the grass snake's (*Natrix natrix*) sites exhibited a small proportion of explained variation. It predicted that at least 20 checks were necessary to infer species absence, which is close to the 26 visits estimated for visual searches in France (Kery 2002). Knowing that at the study site only 38% of the observed individuals were under ATRs, we can deduce that the efficiency of ATR surveys in the case of grass snakes is not much higher than that of walking counts. Compared with other reptiles, the model for individual ATRs showed a considerably greater number of checks and days required until the first record of maximum density populations, which may indicate their irregular use by the grass snake, mostly as occasional shelters. In two species, models were found to be significant only for individual ATRs. The model for *Vipera berus* was similar to that for *Coronella austriaca* indicating that this species is suitable for ATR studies. The model for the Viviparous lizard (*Zootoca vivipara*) showed a small explained variation, with the number of necessary visits to the site and duration of ATR placement being intermediate between those determined for *Anguis fragilis* and *Natrix natrix*; this lizard probably uses ATRs mostly as an occasional thermoregulation enhancer (see below).

Zootoca vivipara was recorded less often in sunny weather compared with fully overcast and variable cloudy conditions (in rainy weather no surveys were conducted). This species is found under ATRs at lower average temperatures than other reptiles (Mutz and Glandt 2004), which can be accounted for both – preference for lower ambient temperatures (relevant data are absent) and sun basking behavior of this heliothermic lizard (Gvoždík 2002). There were no such statistically significant weather preferences observed in other species. ATR use serves a dual purpose for reptiles: ATRs can be used for thermoregulation – average temperatures under iron ATR are several degrees higher than ambient (Mutz and Glandt 2004) and as hiding places. For sheltering under iron ATRs, *Anguis fragilis* preferred air temperatures in the range 19–22 °C irrespective of time or season, and abandoned them at air temperatures below 16 °C. On the contrary, *Coronella austriaca* used ATRs in autumn in cool, overcast weather as well, which suggests that ATRs could also serve as important permanent hiding places irrespective of thermoregulation.

Our study omits evaluation of the minimum necessary number of ATRs or their density per area, because there was no correlation observed between the number of ATRs at a site, and the efforts taken until the first reptile specimen was recorded. This may indicate that the placement of relatively small groups of ATRs (10–20 ATR) at a distance of 10–25 m between individual ATRs is sufficient for the recording of reptiles, which gradually discover them and later prefer profiled iron sheets to natural hiding places due to their better thermal properties.

Habitat overlaps and Coronella austriaca diet

Zootoca vivipara can sense chemical cues of a snake predator and distinguish them from those of a harmless snake (Thoen, Bauwens, and Verheyen 1986; van Damme et al. 1990). In the field study, we did not find evidence that any reptile species, including *Zootoca vivipara*, avoids shelters regularly used by its predator – *Coronella austriaca*. Hence, old chemical cues of *Coronella austriaca* apparently do not deter its potential prey from using the same shelter. On the other hand, there were no cases recorded of an adult snake's co-presence with a smaller one, or with other reptiles except a large adult *Anguis fragilis* or *Natrix natrix*.

The results of the study into the smooth snake population in this area published elsewhere (Čeirāns and Nikolajeva 2014) show that the snake was always found with *Anguis fragilis*, but *Zootoca vivipara* was not recorded at 17% of snake sites. Our survey produced further evidence for the relationship between *Coronella austriaca* and *Anguis fragilis* and only a partial spatial overlap between the habitat of *Coronella austriaca* and that of *Zootoca vivipara*: (i) DFA revealed that the snake habitat niche was fully within that of *Anguis fragilis*, but there was a habitat niche sector from which *Zootoca vivipara* was absent; (ii) *Coronella austriaca* preferred sites abounding with *Anguis fragilis* individuals, but there was no correlation found with *Zootoca vivipara* numbers. This fact shows that sometimes the most important prey species as confirmed by various surveys – *Zootoca vivipara* (Luiselli, Capula, and Shine 1996; Drobenkov 2000; Reading and Jofre 2013; Brown, Ebenezer, and Symondson 2014), is not present or is not significant for the snake.

In the absence of *Zootoca vivipara*, mammals can be consumed as other potential food objects besides *Anguis fragilis*. Shrews can constitute about 30% of snake diets (Reading and Jofre 2013), and they were observed several times under ATRs. Small rodents can constitute up to 10% of snake diets (Drobenkov 2000; Reading and Jofre 2013), and their abundance can increase in degraded bogs (Mazerolle, Drolet, and Desrochers 2001). However, occasional data obtained from regurgitated food items (see introduction section) and captive snake feeding (Čeirāns 2000) do not support the assumption that the given snake population frequently consumes mammalian prey. Other reptile species are very rare in smooth snake diets (Goddard 1984; Luiselli, Capula, and Shine 1996; Drobenkov 2000; Reading and Jofre 2013; Brown, Ebenezer, and Symondson 2014), and we did not find evidence for the feeding of snakes on them in the present study. Hence, all these data strongly indicate that at the study site in the degraded raised bog, *Anguis fragilis* is a very important food object for the smooth snake.

Reptile habitats and bog conservation

Natural, unaffected raised bogs have large areas that are uniformly damp in autumn, winter, and spring, but are arid in summer (Rochefort and Lode 2006). Such habitats have low structural diversity and lack dry wintering places, and our observations indicated that interior parts of such bogs probably lack permanent reptile population. More stable water regime is along the bog periphery, close to mineral soils or close to drained parts of the bog. Grassy embankments also make the bog a more suitable habitat for reptiles because it supports more invertebrates (and consequently lizards), for example carabid beetles (Eversham and Telfer 1994), and offers dry wintering places for reptiles. In our study, both the drained forest edge and the road embankment had a similar positive effect on the presence of reptiles in the most natural part of the bog, where the smooth snake inhabited only ~ 50 m, but *Anguis fragilis* ~ 100 m wide belts along the bog edge. *Zootoca vivipara* can penetrate into the natural raised bog farther than other species, but it is still not clear how much, because its absence under a few most distant ATRs (130–150 m deep) can still be a coincidence.

Drainage for forestry or peat extraction is the main anthropogenic factor in bogs; in Europe 90–95% of peatlands have been altered – degraded or drained (Moore 2002). The bog at the study site was also used for peat extraction some 50–70 years ago, but now vegetation has fully recovered, and the area ranges from intact wet open raised bog in the central part to tall forests developed along its periphery on the drained peat, around old peat pits and in ditched areas. Presently *Anguis fragilis* inhabits a wide habitat spectrum, it is present in tree stands of different height and canopy cover. Occurrence of this species has increased with bog degradation, since it prefers dry habitats and can tolerate afforestation (Čeirāns 2004, 2007; Jofré, Warn, and Reading 2016). The effect of bog degradation on the remaining species is at least neutral, but may have been positive as well.

Thus, *Coronella austriaca* does not penetrate deep into the intact bog (see above).

Zootoca vivipara exhibits a simple habitat selection pattern here. It inhabits various stands with tree cover below the threshold of 30–40% irrespective of tree size. During the study, *Zootoca vivipara* was absent only from ruderal places on rich soil with lush non-bog vegetation. The pattern of habitat use by the two snake species (the smooth snake and the adder) also depends on the tree cover, the preferred tree cover threshold being similar to that preferred by *Zootoca vivipara*. However, unlike the latter, the smooth snake and the adder prefer low (<5 m) stands. Preference for lower stands could be explained as defense against predatory birds such as the common buzzard, which frequently feed on reptiles (Selas, Tveiten, and Aanonsen 2007); low dense stands offer additional cover near the ground level, while taller stands in the study area lack undergrowth and are more open near the ground. Low stand preference was not observed in the third snake species – the grass snake (*Natrix natrix*). Its observation frequency among ATRs (see Figure 4) varied less (like that of *Zootoca vivipara*), which may indicate that the grass snake does not use ATRs as hiding places for a longer time and that it is less selective about ATR location. The grass snake is characterized by great dispersion ability (Madsen 1984; Wisler, Hofer, and Arlettaz 2008), and capability for distant movements in various parts of the drained bog following after food resources – amphibians, which concentrate near peat pits in dry weather, but disperse throughout the bog in wet weather.

Bog habitat restoration is always connected with the closure of drainage ditches and elevation of ground water level (Pfadenhauer and Grootjans 1999; Tuittila, Vasander, and Laine 2000; Rochefort and Lode 2006). The smooth snake and its reptile prey benefit from the lowering of the ground water level and a more stable water regime, and raised bog habitat restoration cannot be recommended for smooth snake sites without an extensive population survey and evaluation of the groundwater level change effect.

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