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HABITAT PREFERENCES AND CONSERVATION OF *VERTIGO GEYERI* (GASTROPODA: PULMONATA) IN SLOVAKIA AND POLAND

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ABSTRACT

The tiny land snail *Vertigo geyeri* Lindholm, 1925 is a rare relict from the Late Glacial, inhabiting treeless spring fens. The main aims of this study were (1) to summarize present knowledge on distribution of *V. geyeri* in Slovakia and in Poland; (2) to analyse its ecology and habitat preferences; and (3) to suggest suitable conservation and management measures for this EUHSD Annex II species. In the course of field research on 122 fens in Slovakia and Poland, carried out between 2001 and 2011, we documented 33 Slovak and 24 Polish sites where this species occurred. Based on analysis of these populations, we identified a strong preference for permanently wet, but not extremely waterlogged, open fen sites with low-productivity nutrient-limited vegetation. The species displayed a unimodal response to calcium concentration in the groundwater, avoiding both calcium-poor *Sphagnum*-dominated fens and extremely mineral-rich and salt travertine fens. All sites in which *V. geyeri* occurs should be protected to prevent any hydrological changes resulting in successional shifts towards more productive and shrubby vegetation. Human-induced eutrophication should be also controlled to ensure the long-term maintenance of viable populations of the species. The locations of all Slovak and Polish fen sites in which *V. geyeri* has been recorded are provided to enable or maintain protection of the species at these sites.

INTRODUCTION

Vertigo geyeri Lindholm, 1925 is a tiny land snail that is protected under Annex II of the EU Habitat Directive (92/43/EEC). The species is usually an inhabitant of treeless spring fens with high and stable groundwater level (e.g. Horsák & Hájek, 2005; Kuczyńska & Moorkens, 2010), but in Finland and Russian Karelia it occurs also in wet, open deciduous woodlands (Valovirta, 2003). *Vertigo geyeri* is a boreo-alpine species, which has a relatively continuous distributional range in Fennoscandia, mainly Sweden and Norway (Pokryszko, 2003; von Proschwitz, 2003). It occurs also at isolated and relic fen sites of Great Britain, Ireland, Switzerland, Italy, Germany, Austria, Slovakia and Poland (Kerney, Cameron & Jungbluth, 1983; Cameron *et al.*, 2003; Holyoak, 2005; Horsák & Hájek, 2005; Vavrová *et al.*, 2009; Hájek *et al.*, 2011). Although the species was formerly regarded as a 'European endemic' (Pokryszko, 2003), it has recently also been found in central Asia (Meng, 2008; Hoffmann *et al.*, 2011).

In Slovakia, *V. geyeri* is limited to the area of the Inner Western Carpathians (Horsák *et al.*, 2007b). Altogether 32 Slovak sites inhabited by the species have been found so far and knowledge of the distribution of the species has been reviewed by Vavrová *et al.* (2009). By contrast, in Poland the only population of the species that has been reliably documented is from one site in the Orawsko-Nowotarska basin close to northwestern Slovakia (Horsák & Hájek, 2005). However, due to its rare and scattered occurrence in ecologically specific habitats of often very small areas of alkaline fens, it is likely that the species is still under-recorded within its whole European distributional range. A similar situation has been revealed recently in other snail species characteristic of spring fens (e.g. *Pupilla pratensis*; Horsák *et al.*, 2010).

The main aims of this paper were: (1) to summarize the results of the malacological surveys on the distribution of *V. geyeri* in Slovakia and Poland and to give an overview of recently discovered populations of the species; (2) to analyse habitat preferences of *V. geyeri*, based on populations studied between 2001 and 2011 in Slovakia and Poland; and (3) to suggest appropriate conservation practices at sites where *V. geyeri* occurs, using an analysis of its ecology.

MATERIAL AND METHODS

Field sampling

The areas within which samples were made lie between 48°52′–49°31′N and 18°34′–20°47′E in Slovakia (Fig. 1) and

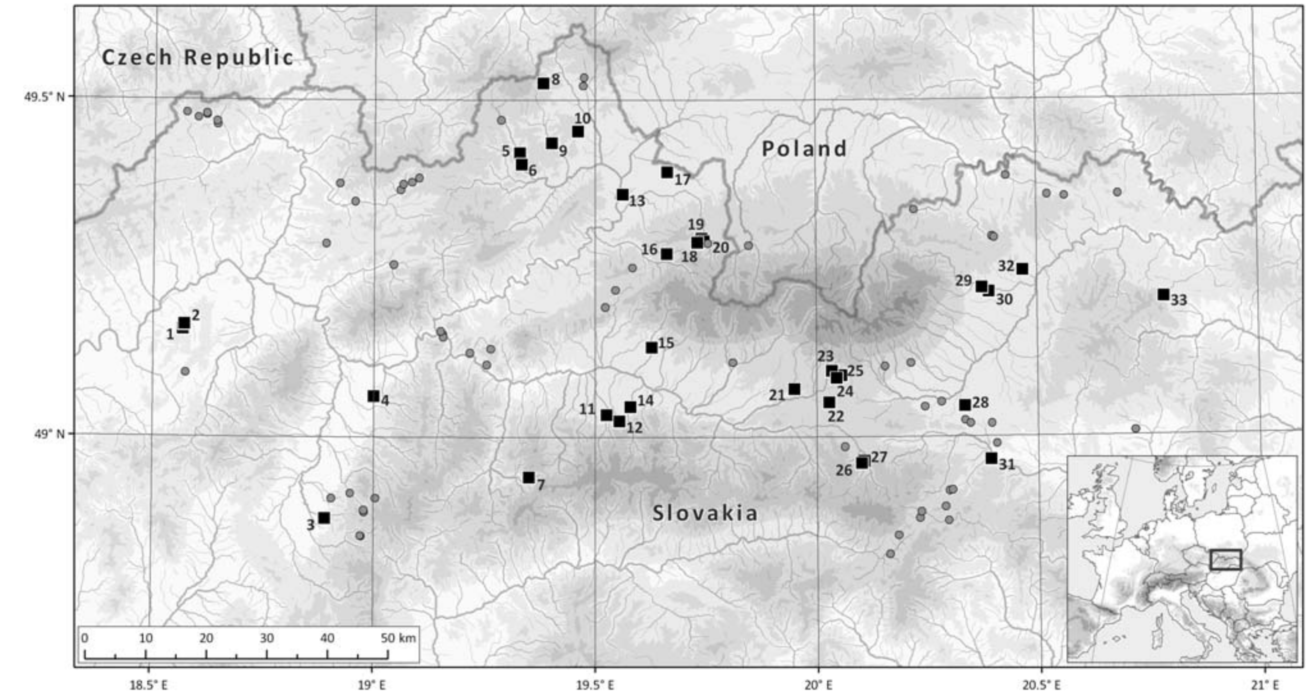

Figure 1. Distribution of 98 study fens in Slovakia showing positions of 33 sites with *Vertigo geyeri* populations (squares). Numbers against *V. geyeri* sites match with the site numbers in the Supplementary Material.

at 49°17′–54°21′N and 19°49′–23°36′E in Poland (Fig. 2). Field work was conducted from 2001 to 2010 in Slovakia and from 2004 to 2011 in Poland. Sites representing potentially suitable habitats for the occurrence of the target species were investigated (i.e. well-preserved treeless spring fens with an undisturbed hydrological regime). Geographical coordinates and altitude of the sites were measured using a GPS in the field. In the central part of each site, a sampling plot of 16 m^2 was defined, in which one sample of 12 l volume comprising the upper soil layer, litter, bryophytes and herbaceous vegetation was collected. Snails were extracted from samples using the 'wet sieving technique' (Horsák, 2003), in which material from each sample is gradually washed through a bowl-shaped sieve (mesh size 0.5 mm) to remove fine soil and coarse plant matter. After drying, shells were separated from the remaining material by hand sorting under a stereo microscope and determined and counted, separating live individuals and empty shells.

The following environmental parameters were compiled for each sampling plot (Table 1). In central parts of the sampling plots, water conductivity and water pH were measured in the microsites best supplied by water, using portable instruments with automatic temperature condensation (CM 101 and PH 119, Snail Instruments, Beroun, Czech Republic). Water conductivity was measured to assess indirectly the concentration of calcium ions in the fens (Sjörs & Gunnarsson, 2002; Hájek *et al.*, 2005). For each site, basic climatic variables (mean annual temperature, maximum temperature of warmest month, minimum temperature of coldest month and annual precipitation) were obtained by using overlays of plot locations with a digital elevation model and climatic maps, based on Miklós (2002) for Slovakia, and by using WorldClim database v. 1.4 (Hijmans *et al.*, 2005) for Poland, in the ArcGIS 8.3 program (ESRI, 2003).

The species composition of the vegetation was recorded in the same 16-m^2 plots. The occurrence and cover of plant species were recorded on the nine-point Braun-Blanquet scale for both vascular plants and bryophytes (van der Maarel, 1979). For each vegetation plot, the average Ellenberg indicator values (Ellenberg IVs) for "light, temperature, continentality, moisture, soil reaction, and nutrients" were calculated using the JUICE program (Tichý, 2002). Ellenberg's plant indicator system (Ellenberg *et al.*, 1992) serves to estimate difficult-to-measure environmental variables and can be utilized effectively for studying ecology of land snails (Horsák *et al.*, 2007a).

Statistical analyses

A total of 122 fen sites in Slovakia and Poland were investigated. Fourteen Polish sites with *Vertigo geyeri* were excluded from the statistical analyses, due to the lack of vegetation data from these sites and also to reduce a potential biogeographical bias because all the sampled sites in Poland contain the species. Those Polish sites which were subjected to the analyses have the same geographical and ecological extent as all sites of the species in Poland. The remaining 108 sites, both with (43 sites) and without (65 sites) the occurrence of *V. geyeri*, were analysed to assess the ecological determinants of the target species. The sites were subjected to Principal Component Analysis (PCA) of a correlation matrix (centred and standardized) based on the 12 explanatory variables to isolate the main ecological variation among all study sites and the relations among individual variables. The sites were classified according to the number of live individuals of *V. geyeri* found. Relationships among site scores on the first three PCA axes and the explanatory variables were analysed using Spearman's rank correlations (r_S).

The responses of *V. geyeri* to the selected environmental gradients were fitted with Generalized Additive Models (GAM; Hastie & Tibshirani, 1990) using Poisson distributions, because usually there are no *a priori* reasons to assume that organisms' responses should follow symmetrical curves (Austin, 1976); the response of species often take more complex shapes. Smooth

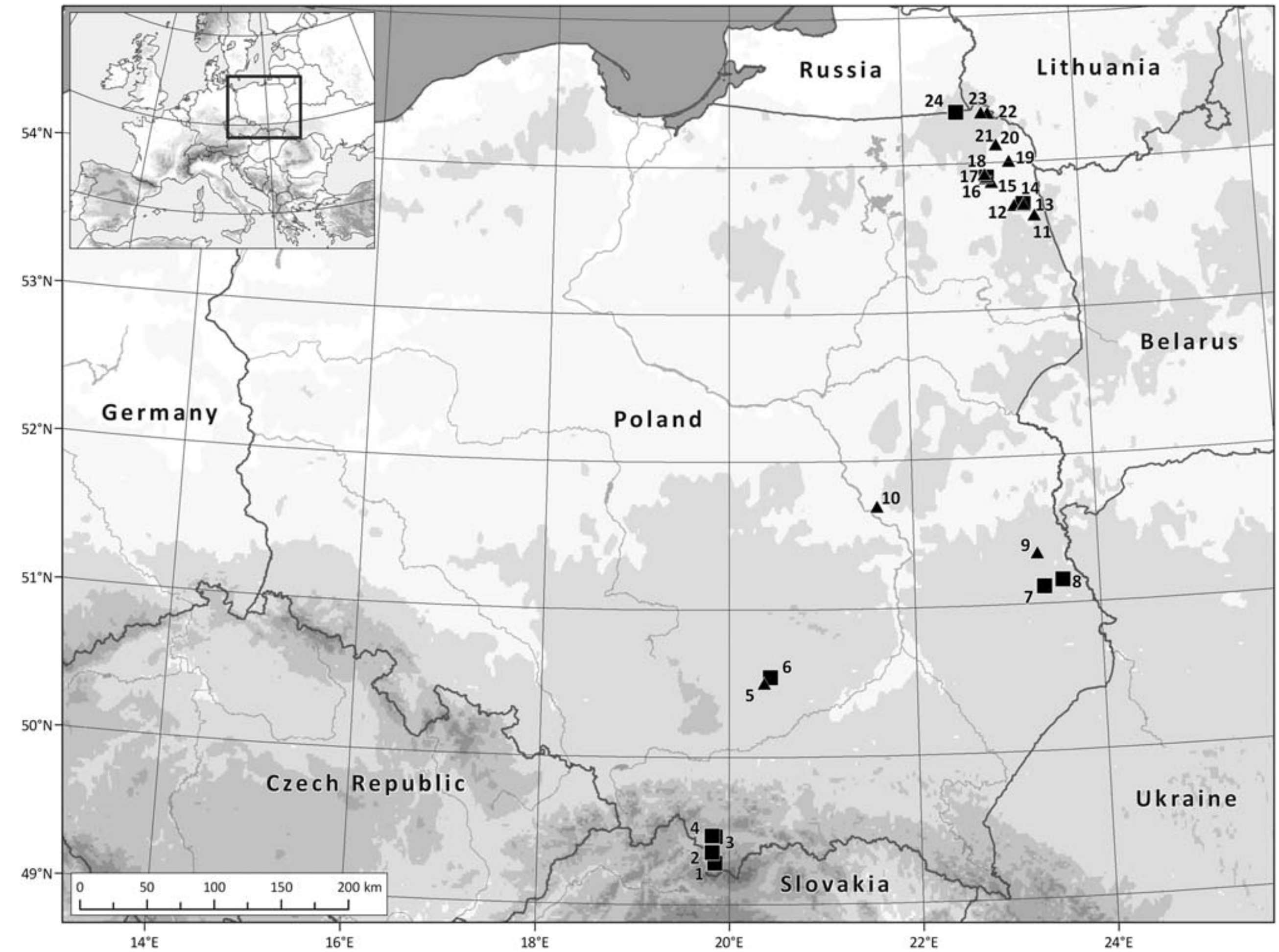

Figure 2. Distribution of 24 known populations of *Vertigo geyeri* in Poland (squares, analysed sites; triangles, sites not included in the statistical analyses). Numbers of sites match with the site numbers in the Supplementary Material.

Table 1. Descriptive statistics for variables used in the analyses for 43 sites with occurrence of *Vertigo geyeri*.

	Median	Mean	Standard deviation	Min.	Lower quartile	Upper quartile	Max.
Water pH	7.1	7.0	0.6	4.7	6.8	7.4	8.1
Water conductivity (μS/cm)	360	363	190	33	201	478	918
Ellenberg IVs for temperature	4.8	4.8	0.3	4.1	4.6	5.0	5.4
Ellenberg IVs for moisture	8.1	8.1	0.3	7.4	7.9	8.4	8.6
Ellenberg IVs for soil reaction	6.2	6.1	0.7	4.7	5.4	6.8	7.5
Ellenberg IVs for nutrients	2.8	2.9	0.4	2.3	2.6	3.3	4.0
Ellenberg IVs for light	7.5	7.5	0.2	7.1	7.4	7.7	7.9
Ellenberg IVs for continentality	3.5	3.5	0.3	3.0	3.3	3.7	4.1
Mean annual temperature (°C)	6.1	6.1	0.8	4.9	5.4	6.5	7.8
Max. temperature of warmest month (°C)	21.5	21.5	1.2	19.7	20.4	22.3	23.7
Min. temperature of coldest month (°C)	−8.7	−8.7	0.6	−9.5	−9.1	−8.4	−7.1
Annual precipitation (mm)	902	856	151	525	737	986	1057

term complexity was selected using the Akaike Information Criterion (AIC). This criterion attempts to measure model 'parsimony' using the number of model degrees of freedom (lowest AIC value = highest parsimony). All options were chosen based on the recommendations of Lepš & Šmilauer (2003: 124–139). The CANOCO v. 4.5 package (ter Braak & Šmilauer, 2002) was used for ordination techniques and GAM modelling, and STATISTICA 7 (Hill & Lewicki, 2007) was used for unidimensional analyses. In cases of multiple testing, sequential Bonferroni corrections of the significance level were used (Holm, 1979).

RESULTS

Of the 122 fen sites studied, *Vertigo geyeri* was recorded at 33 sites in Slovakia and 24 sites in Poland (Figs 1 and 2). The distribution of the species in Slovakia has been extensively studied in the past few years and all the Slovak sites, with one

Table 2. PCA of 12 explanatory variables established for each of 108 analysed fen sites.

PCA axes	1st axis		2nd axis		3rd axis	
Eigenvalues	0.324		0.200		0.177	
	r_S	*P*	r_S	*P*	r_S	*P*
Water pH	0.36	**<0.001**	0.57	**<0.001**	−0.30	**0.002**
Water conductivity	0.68	**<0.001**	0.35	**<0.001**	−0.32	**<0.001**
Ellenberg IVs for temperature	0.56	**<0.001**	−0.21	0.024	0.38	**<0.001**
Ellenberg IVs for moisture	−0.19	0.049	−0.54	**<0.001**	−0.53	**<0.001**
Ellenberg IVs for soil reaction	0.37	**<0.001**	0.62	**<0.001**	−0.33	**<0.001**
Ellenberg IVs for nutrients	0.19	0.042	0.47	**<0.001**	0.74	**<0.001**
Ellenberg IVs for light	0.22	0.022	−0.12	0.227	−0.87	**<0.001**
Ellenberg IVs for continentality	0.06	0.528	0.31	**<0.001**	0.03	0.746
Mean annual temperature	0.87	**<0.001**	−0.47	**<0.001**	0.13	0.164
Max. temperature of warmest month	0.90	**<0.001**	−0.42	**<0.001**	0.10	0.277
Min. temperature of coldest month	0.67	**<0.001**	−0.58	**<0.001**	0.28	**0.003**
Annual precipitation	−0.66	**<0.001**	−0.07	0.462	0.18	0.060

Significant correlations after Bonferroni correction ($P < 0.0033$) are in bold. Correlations of explanatory variables with the first three PCA axes (r_S) and their significances (*P*) are shown. Sum of all eigenvalues was standardized to 1.0 and sum of explained variation by the first three PCA axes was 70.1%.

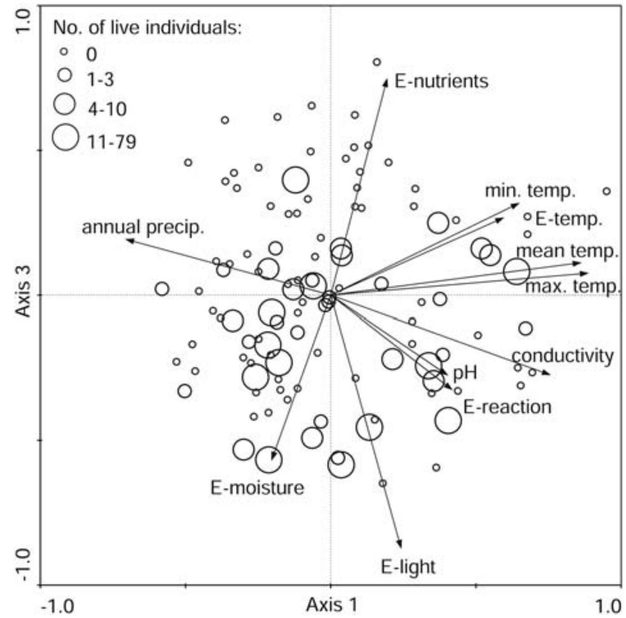

Figure 3. PCA ordination plot of 108 studied fens based on 12 explanatory variables (Table 1); sites are potted on the first and the third ordination axes. Only those explanatory variables that were significantly correlated with the first and third axis are shown. Size of circles corresponds with numbers of live *Vertigo geyeri* individuals. The first ordination axis explained 32.4% and the third 17.7% of total variation.

exception, were previously known. On the contrary, only one site in Poland was previously known (Horsák & Hájek, 2005) and *V. geyeri* was newly discovered at 23 fens. Detailed information about all sites containing *V. geyeri* is given in the Supplementary Material. Sites without the species were mainly published in Horsák (2005a) and Vavrová *et al*. (2009).

The PCA using 12 explanatory variables revealed a complex ecological gradient of mineral richness and climate, expressed by the first two ordination axes (Table 2). The third axis was the most associated with herb-layer productivity and the proportion of light-demanding plant species, estimated by Ellenberg IVs for nutrients and light. The position of sites on the first and third PCA axes (Fig. 3) showed that *V. geyeri* reached the highest abundances at moist, low-productivity fens with sparse vegetation cover (i.e. higher Ellenberg IVs for moisture and light, and lower for nutrients).

Altogether five of the 12 investigated ecological variables had significant effects on the population densities of *V. geyeri* (Fig. 4). The strongest relationship was found for Ellenberg IVs for moisture (Fig. 4A); the abundances increased towards sites with a high and stable groundwater level, but the species avoided the most waterlogged sites. We observed significantly decreasing relationship between Ellenberg IVs for nutrients and abundances of *V. geyeri*, which showed the species' preference for sites with the low-productivity, nutrient-limited vegetation (Fig. 4B). This is in keeping with the species' response to Ellenberg IVs for light; densities of the species were higher in sites with higher proportion of light-demanding plants (Fig. 4C). Significant responses to both conductivity and Ellenberg IVs for soil reaction confirmed a unimodal response to mineral concentration (mainly calcium and magnesium) in the groundwater (Fig. 4D, E). We note that this overall analysis yields the same results as for Slovakia alone (data not shown); the addition of Polish sites selected for their apparent suitability for the species merely strengthens the trends.

The species' occurrence in spring fens varied between the different vegetation types (Table 3). *Vertigo geyeri* reached the highest abundances in calcareous tufa-forming fens of the *Caricetum davallianae* association and was found at 50% of all investigated fens of this vegetation type. With almost the same frequency the species occurred also in fens with vegetation of *Sphagno warnstorfii–Tomenthypnion nitentis* alliance, though its population sizes at these less calcareous sites were notably lower. The snail was also found at sites of *Campylio stellati–Caricetum lasiocarpae*, *Carici flavae–Cratoneuretum falcati* and *Valeriano simplicifoliae–Caricetum flavae* associations (Table 3); however, the low number of sites belonging to these vegetation types does not permit reliable generalization of the species' preferences.

DISCUSSION

Current distribution of Vertigo geyeri *in Slovakia and Poland*

Intensive surveys of Slovak fens during the last 10 years show that the Slovak part of the Inner Western Carpathians may well be a Central European stronghold for *V. geyeri* (Vavrová *et al*., 2009). The number of recently known sites stands at 33 and it is likely that more will be found in the future. By contrast, there is very little previous information from Poland. *Vertigo geyeri* was recorded in error from the Świętokrzyskie Mountains (see Pokryszko, 1990), but despite its occurrence in countries to the north, east and west, the only reliable record of *V. geyeri* was from the Orawsko-Nowotarska basin, southern Poland (Horsák & Hájek, 2005). The 23 new sites documented here show that the distribution of *V. geyeri* throughout Poland is much wider than previously thought. A similar increase in the number of known sites for the species occurred in Great

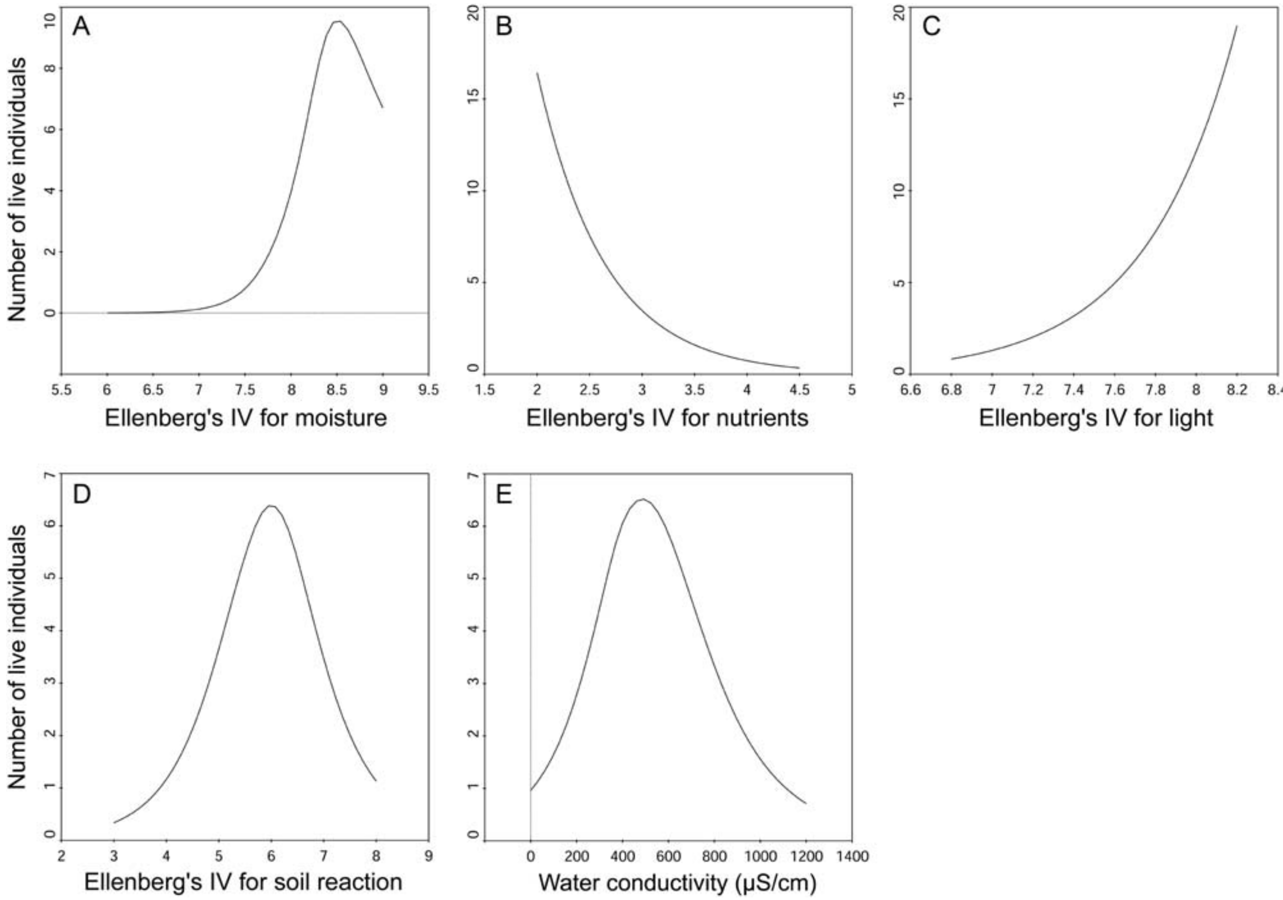

Figure 4. Species response curves of *Vertigo geyeri* based on 108 fen sites in Slovakia and Poland. Response curves were compiled using GAM. **A.** Ellenberg's moisture, $P < 0.001$. **B.** Ellenberg's nutrients, $P = 0.005$. **C.** Ellenberg's light, $P = 0.033$. **D.** Ellenberg's soil reaction, $P = 0.026$. **E.** Water conductivity, $P = 0.019$.

Table 3. Classification of all 108 analysed fens into three structural habitat types and seven vegetation types: number of sites in each vegetation type and frequency of sites at which *Vertigo geyeri* was recorded (%) are given.

Structural habitat type	Vegetation type	No. of sites	Frequency (%)	Median abundance
Calcareous fens	*Glauco-Trichophoretum pumili*	6	0	0.0
	Carici flavae-Cratoneuretum	22	36	2.5
	Caricetum davallianae	28	50	11.0
Extremely rich fens	*Valeriano-Caricetum flavae*	16	25	3.5
	Campylio-Caricetum lasiocarpae	6	83	3.0
Rich fens with calcitolerant *Sphagna*	*Sphagno-Tomenthypnion*	25	48	3.0
	Sphagno recurvi-Caricion canescentis	5	0	0.0

Median abundance of live individuals at each vegetation type was calculated only from sites with the occurrence of the species.

Britain as a result of new expert surveys (Cameron & Killeen, 2001). There are other fens of similar habitat types elsewhere in Poland, which have not been malacologically explored so far and at which the occurrence of the species may be expected. Our findings reinforce the conclusions of Pokryszko (2003) that *V. geyeri* occupies certain fen types across northern Europe and is not a strict arctic-alpine species. Future studies in Poland should focus on fens with vegetation of *Caricetum davallianae* association, at which *V. geyeri* reaches the highest abundances (Table 3). The occurrence of the species may also be expected at fens with vegetation of *Campylio-Caricetum lasiocarpae*, *Valeriano-Caricetum flavae*, *Sphagno-Tomenthypnion* and *Carici flavae-Cratoneuretum*, although population densities of *V. geyeri* at sites of these vegetation types appear to be lower than in *Caricetum davallianae* fens.

Ecology and habitat preferences

Previous studies showed that *V. geyeri* possesses rather broad ecological amplitude along the gradient of mineral richness (Horsák & Hájek, 2005; Vavrová *et al.*, 2009). It frequently inhabits calcareous spring fens with tufa formation, but can also be found in fens only moderately rich in calcium, which can support the occurrence of calcitolerant *Sphagnum* species. In such fens, *V. geyeri* always avoids patches with a continuous *Sphagnum* layer and it is restricted to areas richer in calcium, which are fed more by mineral-rich groundwater than by precipitation (von Proschwitz, 2003; Horsák & Hájek, 2005; Vavrová *et al.*, 2009). The same response to calcium concentration was observed here in Slovak and Polish populations of *V. geyeri*. The snail displayed a unimodal response to the mineral richness gradient with an optimum shifted to more calcium-rich sites, as confirmed using the Ellenberg's soil reaction and directly measured water conductivity (Fig. 4D, E). In summary, *V. geyeri* avoids both mineral-poor *Sphagnum*-dominated fens and also extremely calcareous travertine fens, and its optimum lies in the base-rich sites with slight tufa precipitation (see also Horsák, 2006). However, the response to water pH was not significant, probably because in the studied range of the mineral richness gradient, water conductivity and Ellenberg's soil reaction reflect the calcium concentration much more precisely than does pH (Sjörs & Gunnarsson, 2002; Horsák, 2006; Horsák *et al.*, 2007a).

The significant response to Ellenberg's moisture confirmed that stable water regime and permanently high level of groundwater at sites are the most important factors for the long-term survival of *V. geyeri* (Fig. 4A). However, extremely waterlogged sites were not preferred by *V. geyeri*, as the population densities declined towards sites with a predominance of high-moisture demanding plant species. Although *V. geyeri* crawls on the leaves and stems of low-growing sedges, it does not climb up the taller stems of emergent plants, unlike *V. moulinsiana* (Ausden *et al.*, 2005). We observed that *V. geyeri* favoured sites with high values of Ellenberg's light and low Ellenberg's nutrients (Figs 3, 4B, C). Increasing values of Ellenberg's nutrients reflect the increasing representation of nutrient-demanding plants, i.e. meadow forbs and grasses, and positively correlates with above-ground vegetation biomass production (Schaffers & Sýkora, 2000). The increasing value of Ellenberg's light refers to increasing representation of light-demanding plants and relates to the site's openness and density of vegetation layer (Horsák *et al.*, 2007a). The monotonic increasing response of *V. geyeri* to light and monotonic decreasing response to nutrients indicate that the species prefers nutritionally poor fens with a sparse vegetation cover. Similar ecological preferences were recently documented for *Pupilla alpicola* (Horsák, Škodová & Cernohorsky, 2011), which is also considered as a glacial relic species and threatened fen habitat specialist.

The occurrence of *V. geyeri* in the Western Carpathians reflects both suitable habitat conditions and historical continuity of the sites throughout the Holocene (Horsák, 2005b; Horsák *et al.*, 2007b; Hájek *et al.*, 2011). In central Europe *V. geyeri* represents a rare relic from wet glacial periods (Ložek, 1992) and therefore it occupies areas with Pleistocene/Holocene continuity of spring fens. On that account, the species is missing in some areas, where the open treeless state of fens is relatively young and relates to human activities, e.g. in the Outer Western Carpathians (Hájek *et al.*, 2005), despite a high frequency of ecologically suitable habitats (see Horsák *et al.* 2007b; Hájek *et al.*, 2011). Thus, not all sites with apparently suitable environmental conditions hold the species; those that do are generally those that have preserved their character throughout the Holocene. The conservation of such sites is the major requirement to maintain favourable conservation status for the species.

Because *V. geyeri* occurred in all the analysed sites from Poland, there was a potential risk of geographical bias in our statistical analyses. Therefore, we ran the same analyses based on Slovak sites and the results remained exactly the same (data not shown). This is probably due to the fact that Polish sites of the species posses the same ranges of ecological parameters as do the Slovak sites. It also revealed that species responses to the studied ecological factors express geographically stable patterns.

Table 4. Conservation and management of all 57 fen sites in Slovakia and Poland with occurrence of *Vertigo geyeri*.

Type of protection and management	Slovakia ($n = 33$)	Poland ($n = 24$)
Sites protected by law*	70% (23 sites)	42% (10 sites)
Sites included in NATURA 2000 network	52% (17 sites)	92% (22 sites)
Sites with (at least irregular) management	52% (17 sites)	17% (4 sites)

*National Park, Landscape Park, National Nature Reserve or Nature Reserve.

Conservation and site management

Vertigo geyeri has very specific microhydrological requirements and it acts as a sensitive indicator of stable habitat conditions. These requirements and possible threats to its habitats have been reviewed in several works (e.g. Cameron *et al.*, 2003; Holyoak, 2005; Vavrová *et al.*, 2009; Kuczyńska & Moorkens, 2010). Our results reinforce the conclusions of these studies. In particular, changes in the water regime and large groundwater-level fluctuations have a strong negative impact on the species and can lead to its rapid loss. Therefore, any activities altering hydrological conditions at target sites or in their catchments (drainage, agriculture etc.) should be avoided.

Populations of *V. geyeri* are also threatened by successional changes after cessation of traditional management practices, which can result into overgrowing and shading of the habitat by more productive, broad-leaved vascular plants (Skeffington *et al.*, 2006). On the other hand, heavy grazing, trampling and mowing can have damaging effects as well (von Proschwitz, 1998).

Within the European Union, *V. geyeri* is a species listed under Schedule II of the EU Habitats and Species Directive, requiring member states to maintain favourable conservation status for the species (Cameron *et al.*, 2003). Table 4 summarizes the present status of sites known to contain *V. geyeri* in Poland and Slovakia. In the latter, 70% of sites are protected by law, and more than half are subject to appropriate management. The situation in Poland is less satisfactory, although the majority of sites are included in the NATURA 2000 network. Lack of local management, resulting in secondary succession and invasion of shrubs, trees or reeds, is not the only threat to these fens. Several sites in Slovakia and Poland are seriously endangered also by direct human activities, such as exploitation, peat extraction, drainage or building in the adjacent areas.

SUPPLEMENTARY MATERIAL

Supplementary Material is available at *Journal of Molluscan Studies* online.

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