COEXISTENCE OR SPATIAL SEGREGATION OF SOME VERTIGO SPECIES (GASTROPODA: VERTIGINIDAE) IN A CAREX RICH FEN IN CENTRAL POLAND?

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Abstract The paper describes the occurrence of an assemblage of Vertigo, composed of four species, Vertigo moulinsiana, V. angustior, V. antivertigo and V. pygmaea, in a small patch of habitat in the degraded environs of Konin, central Poland. The survival of this assemblage in an area strongly affected by human impact has resulted from the microhabitat diversity in the fen and the high quality of the surrounding matrix. Relatively high numbers of V. angustior in the temporarily disturbed part of the fen additionally show that it can inhabit areas subject to occasional and extensive human use. Spatial relations between fen-dwelling species, especially between the most abundant V. moulinsiana and V. angustior, were considered in the context of their preferences for particular habitat conditions relating to the ground moisture levels and microclimate. These seemingly coexisting species were almost completely separated in space, both vertically and horizontally, occupying different meso- and microhabitats.

Key words terrestrial snails, microhabitat selection, habitat fragmentation, Vertigo moulinsiana, Vertigo angustior

Introduction

Many of the European Vertigo species (e.g. V. moulinsiana, V. angustior, V. geyeri) are restricted to primary, moist and calcium-rich open habitats (Pokryszko, 1990; Cameron et al., 2003; Vavrová et al., 2009; Książkiewicz, 2010). Nowadays, such habitats are strongly fragmented and degraded in many areas (Hájek et al., 2002; Killeen, 2003; Vavrová et al., 2009). There is still little data on how such fragmentation influences these snails and to what extent the particular Vertigo species and their assemblages can survive in small patches of habitats.

Recently knowledge of Vertigo species has been greatly enhanced. The increased interest in them has mainly been related to the fact that several species are threatened and four are listed in the Annexes of the EU Habitats Directive (Cuttelod et al., 2011) and are therefore strictly protected. Recently published data mainly concern new localities, some habitat requirements, assessment of the population and habitat conservation status and monitoring issues (e.g. Killeen & Moorkens, 2003; Beran, 2006; Książkiewicz, 2009; Schenková et al., 2011). On the other hand, knowledge of *Vertigo* biology, and especially of the coexistence and spatial relationships between species, is still insufficient.

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This paper describes the occurrence of a *Vertigo* assemblage in a small, seemingly relict patch of a habitat in the context of the spatial relations of fen-dwelling species and the preferences of these snails for differing ground moisture levels. Our sampling method and the derived picture of spatial distribution allowed us to address the following questions:

- Is and to what extent the ground moisture level decisive for spatial distribution of fendwelling Vertigo species?
- Do fen-dwelling Vertigo species coexist or are they segregated spatially?

MATERIAL AND METHODS

Study site Vertigo species were recorded during research on malacofauna conducted within the project "The evaluation and revitalization of Konin Lakes for regional development", at the request of the regional authorities. During these studies an interesting Carex rich fen was found and thoroughly checked. First data were obtained in May and the main study was carried out in August and September 2011.

The fen (0.05 ha) is situated in a complex of old post-excavation peaty pools, fens and meadows south of Kepa village (52°18′20.5″ N 18°19′08.1″ E). It is surrounded by a willow carr and meadows (Figs 1a, c, 2). The habitat is characterised mainly by fairly dense and dense Carex acuta

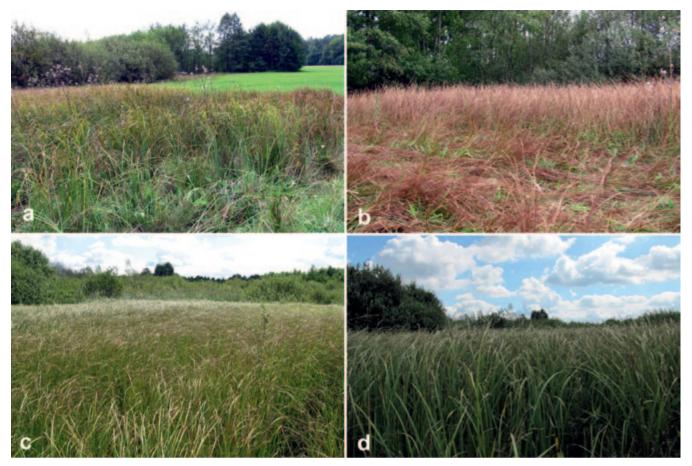


Figure 1 The habitat of four Vertigo species near Kepa, central Poland – the Carex rich fen with a surrounding matrix. a and b – the drier part of the fen with (on b) fragments partly disturbed by a tractor, c and d – the wetter part of the fen: a general view and texture of vegetation.

L. with some admixtures of Equisetum fluviatile L., Lysimachia vulgaris L., Lythrum salicaria L., Cirsium arvense (L.) Scop., Geum rivale L., Galium sp., Sanguisorba officinalis L., Plantago lanceolata L., Mentha arvensis L., and with Calliergonella cuspidata (Hedw.) Loeske and Drepanocladus polycarpos (Bland. ex Voit.) Warnst. in the moss layer. Two parts are clearly recognisable in the fen. The drier part, partly bounded with meadows (Figs 1a, b, 2), is composed of lower (70–100 cm) and slightly looser C. acuta with a significant admixture of eight other plants. The wetter part is distinguished by a more uniform, lawn-like texture of vegetation (Fig. 1c, d) consisting of a denser and taller (130–150 cm) stand of C. acuta and only a small admixture of three other plant species (E. fluviatile, L. vulgaris, L. salicaria). This division into the pure Carex fen and the Carex fen enriched with meadow plants approximately reflects a difference in the ground moisture level. The former part is damp or wet and the latter is dry according to the scale of Killeen & Moorkens

(2003, see below). The soil was slightly alkaline (pH 7.81) and the water calcium concentration was moderate (100 mg/l).

The outer fragment of the fen, i.e. that adjacent to the meadow, was disturbed during the studies (Fig. 2). C. acuta and other plants were crushed onto the ground (Fig. 1b) by a tractor repeatedly turning round to return to the neighbouring meadow. This area is probably disturbed in this way each year and an older satellite photograph from 2008 (Google Earth maps) showed that it had even been partly mowed.

Sampling methods The samples were taken (Fig. 2) as follows.

along a 22-metre-long transect set up in the undisturbed part of the studied fen (the main study area) along the moisture-gradient, from the driest section to the wet section (28 samples); further permanently inundated parts were not studied; the distances between sample sites were between 1 and 2 metres;

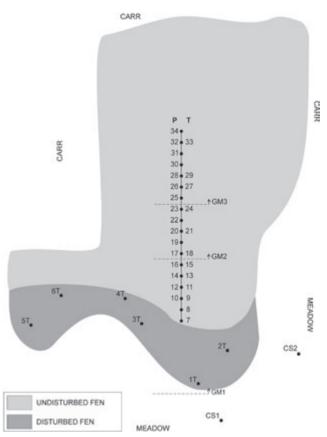


Figure 2 Sample sites with their numbers (1–34) and kind of sample (P – plant, T – thatch & litter), control sample sites (CS1 and 2), a transect and ground moisture level (GM1, 2, 3) according to the five point scale (Killeen & Moorkens, 2003) in the studied *Carex* rich fen near Kępa (central Poland) divided into an undisturbed part (lighter) and a disturbed part (darker).

- in randomly selected sites in a supplementary area, i.e. in the disturbed outer part of the fen, adjacent to the meadow (6 samples);
- in randomly selected sites in the moist meadow a few metres from the fen (2 control samples).

The samples were taken in two ways: (i) plant samples (P) – individuals hand-collected only from plants above the ground; (ii) thatch and litter samples (T) – individuals collected from thatch and litter, within 25×25 cm quadrats (Ökland frames).

Out of 36 samples, 16 plant samples were taken in the main transect and 20 thatch and litter samples were taken in the main, supplementary and control areas. The height above the ground level and the kind of substrate were recorded for each hand-collected individual.

In each sample the ground moisture level was determined according to a scale of 1–5 (Killeen &

Moorkens, 2003): 1 – dry, no visible moisture on ground surface; 2 – damp, ground visibly damp, but water does not rise under pressure; 3 – wet, water rises under light pressure; 4 – very wet, pools of standing water, generally less than 5 cm deep; 5 – site under water, entire sampling site in standing or flowing water over 5 cm deep. Additionally, the maximum height of vegetation was measured in each sample in the undisturbed area.

RESULTS

Four species of *Vertigo* were recorded in the fen: Vertigo (Vertigo) antivertigo (Draparnaud 1801), Vertigo (Vertigo) moulinsiana (Dupuy 1849), Vertigo (Vertigo) pygmaea (Draparnaud 1801) and Vertigo (Vertilla) angustior Jeffreys 1830 (Table 1, Fig. 3, Appendix 1). Additionally, a fifth species, Vertigo (Vertigo) pusilla O.F. Müller 1774 (1 individual and 1 fresh shell in a litter sample) was found nearby, in a mixed forest separated from the fen by a 40-metre-wide meadow. As it occurred in a completely different habitat, it has not been considered in further analyses. In control samples taken in the meadow no vertiginids were found. V. moulinsiana was generally the most abundant species. Considering all the material - both plant and thatch-litter samples - it constituted 72.1% of all Vertigo individuals (Table 1). The percentage of *V. angustior* was significantly lower (21.6%), but still high in comparison with V. antivertigo (3.7%) and *V. pygmaea* (2.6%).

The plant samples were clearly dominated by *V. moulinsiana* (94.4%) with a small admixture of *V. antivertigo* (3.2%) and *V. angustior* (2.4%). The structure of dominance in the thatch-litter samples was different, with *V. angustior* constituting 59.4%, *V. moulinsiana* 28.1%, *V. pygmaea* 7.8% and *V. antivertigo* 4.7%. The frequency in plant samples was significantly higher for *V. moulinsiana* 81.2%, than for *V. antivertigo* 25%. *V. angustior* was found in only 6.2%. The highest frequency in the thatch-litter samples was reached by *V. angustior* (61.1%), while the frequency of other species was significantly lower: *V. moulinsiana* 27.8%, *V. antivertigo* 16.7%, *V. pygmaea* 11.1%.

Vertigo angustior occurred almost exclusively in thatch and litter: the lowest layer, up to 10 cm above the ground. Only three individuals (2.4%) were found on plants in the transitional layer (11–20 cm above the ground) containing the lowermost parts of emergent stems and blades

Table 1 Number of recorded individuals of particular *Vertigo* species in the *Carex* rich fen near Kepa (central Poland).

Species	Number of individuals	Number of individuals in	Total number of individuals		
	in plant samples	thatch-litter samples -	Adult	Juvenile	Total
Vertigo antivertigo	4	3	7		7
Vertigo moulinsiana	119	18	44	93	137
Vertigo pygmaea		5	5		5
Vertigo angustior	3	38	39	2	41
Totals	126	64	95	95	190

with still numerous broken dead leaves. Very rare individuals of *V. pygmaea* inhabited only the lowest thatch-litter layer. In *V. moulinsiana*, 15.3% of individuals were recorded in the thatch-litter layer and 19.8% of individuals in the transitional zone. Most of the population (64.9%) was found higher, above 20 cm and up to 88 cm, in the zone dominated by erect living stems and leaf-blades. Three individuals of *V. antivertigo* (42.9%) were sampled in the thatch-litter layer, while four others (57.1%) were noticed in the transitional layer.

Many of the individuals of V. moulinsiana found on emergent leaf blades occupied an indented part of their upper surface forming a "channel" along the central vein. This preference was recognisable though not assessed quantitatively. More than two-thirds of V. moulinsiana individuals (67.9%) were juvenile, while the percentage of juveniles in V. angustior was much lower at 4.9% (Table 1). All the sampled individuals of *V. antivertigo* and *V. pygmaea* were adult. The Vertigo species were accompanied by other terrestrial snail species: Euconulus (Euconulus) praticola (Reinhardt 1883), Trichia (Trichia) hispida (Linnaeus 1758), Vallonia pulchella (O.F. Müller 1774), Succinea putris (Linnaeus 1758), Cochlicopa lubricella (Rossmässler 1835), Zonitoides (Zonitoides) nitidus (O.F. Müller 1774), and water snail species: Segmentina nitida (O.F. Müller 1774), Anisus spirorbis (Linnaeus 1758), Galba truncatula (O.F. Müller 1774).

DISCUSSION

The broad environs of Konin have been greatly disturbed and altered due to many years of brown coal opencast mining and energy production. The occurrence of *V. angustior* and *V. moulinsiana*, which are believed to inhabit primary habitats (Pokryszko, 1990; Kerney, 1999;

Vavrová *et al.*, 2009), is thus noteworthy. What is more, four *Vertigo* species co-occurred at this locality of only 0.05 ha, and both *V. angustior* and *V. moulinsiana* were abundant. This strongly suggests the long-term survival of these snails in this rich fen or at least in this complex of wetlands within the otherwise very disturbed area.

The co-occurrence of vertiginids at the same locality has been frequently reported, for example two to five Vertigo species were recorded at 19 localities in Slovakia and at one site in southern Poland (Horsák & Hájek, 2005). In northwestern Poland – where two to four species were found at six localities (Książkiewicz, 2010) – the co-occurrence was mostly observed in a mosaic habitat larger than 1 ha, including diverse plant communities often with ecotone zones between open areas and carr or forest. The fen near Kepa, inhabited by four co-occurring species, was much smaller than 1 ha and relatively homogeneous, including only two forms of Caricetum acutae. This shows that even a small patch of appropriate habitat can be sufficient for the survival of vertiginids – not only a single species but even a quite rich assemblage - in a highly disturbed region. Strong fragmentation of habitats does not have to be, therefore, tantamount to the extinction of Vertigo species and their assemblages. The high quality of the habitat and surrounding matrix seems to be decisive for preserving both the local richness and abundance of vertiginids.

The studied fen is situated in an area including willow and alder carrs, post-excavation peaty pools, extensively grazed moist meadows and the nearby Licheń Lake. Such a surrounding matrix provides a relatively stable water regime with a high ground water level, which is crucial for some vertiginids, especially for *V. moulinsiana* (Killeen, 2003a; Tattersfield & McInnes, 2003). The surrounding matrix seems to be an



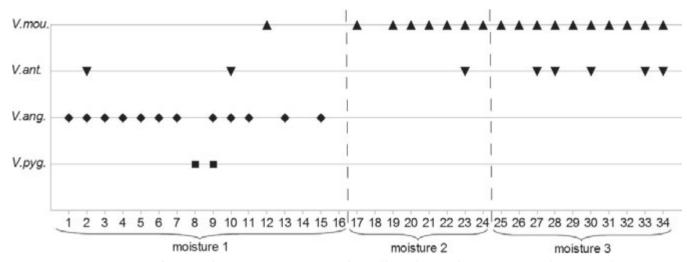


Figure 3 Occurrence of particular Vertigo species in the collected samples (1-34) in relation to the moisture level of the habitat (according to the scale by Killeen & Moorkens, 2003) in the Carex rich fen near Kepa (Central Poland). Abbreviations of species names: V. mou. – Vertigo moulinsiana, V. ant. – Vertigo antivertigo, V. ang. – Vertigo angustior, V. pyg. – Vertigo pygmaea.

important, though underestimated factor for the conservation status of vertiginids in a landscape greatly altered by human impact. The moderate calcium content in the study area also certainly favours the occurrence of Vertigo species, which are mostly known to be calciphile (Pokryszko, 1998; Drake, 1999; Vavrová et al., 2009). However, the meso- and microhabitat diversity seems to be the key factor for the co-occurrence of as many as four *Vertigo* species in such a small area.

The most abundant species, *V. moulinsiana* and V. angustior, inhabited different meso- and microhabitats in the fen. V. moulinsiana occurred in the wet and damp parts of the fen, with a significant dominance of C. acuta. V. angustior occupied relatively dry parts, where C. acuta was accompanied by a large admixture of other plant species. Even at this level, an almost complete spatial segregation was noticed (Fig. 3). The different preferences of these species for ground moisture level have been reported at other localities (e.g. Cameron et al., 2003; Książkiewicz, 2008, 2009), but the local ranges of species and their segregation have not previously been described in detail. Apart from horizontal spatial separation, vertical spatial segregation – commonly known for these species (e.g. Pokryszko, 1990; Cameron et. al., 2003; Lipińska, 2010) – was recorded at the study site. V. angustior was a thatch-and-litter species which sometimes climbed plant elements up to several centimetres high, while V. moulinsiana was a high climber ascending emergent stems and blades during the vegetation period with

only few individuals present in thatch. The horizontal separation and significant vertical segregation may indicate a kind of resource partitioning between these species. They possibly use the same resource, as food (fungi), in different physical locations at the same time. This situation indicates that seemingly coexisting Vertigo species are actually clearly segregated or even separated in space.

The recognised preferences of *V. moulinsiana* for damp and wet habitats perfectly match with the ecology of this species (Pokryszko, 1990; Cameron et. al., 2003; Killeen, 2003b; Ksiażkiewicz, 2010). On the contrary, Lipińska et al. (2011) recorded the highest density in sedge in "dry" conditions. However, there is most probably no difference between the "damp" conditions described by us and the "dry" conditions reported by Lipińska et al. (2011). This inconsistency only results from applying different scales for ground moisture level. Lipińska et al. (2011) used the old three point scale by Stebbings & Killeen (1998), where the lowest category "dry" is broad and comprises all the conditions with water not appearing after stepping on the ground. This rather imprecise scale was then modified by Killeen & Moorkens (2003) to the five point scale used in our study. "Dry" conditions according to the old scale comprise two ground moisture levels in the new scale, i.e. dry and damp conditions. In our opinion, the scale by Killeen & Moorkens (2003) much better reflects actual differences in microhabitat preferences between vertiginids,

and hence is much more useful. According to the old scale, all the *Vertigo* species recorded in our study, occurred in "dry" conditions. Only the new scale allowed us to account for the almost complete spatial separation between *V. angustior* and *V. moulinsiana*.

The high moisture requirements of *V. moulin*siana are not in opposition to its microhabitat preferences. The species inhabits a seemingly unfavourable niche, i.e. strongly insolated open microsites above the ground. In fact, sedge fens with their dense, even-topped, lawn-like texture and high ground water level resemble a miniature jungle providing an appropriate microclimate with high humidity. Such microclimatic conditions are favourable for hygrophilous snails not only directly, but probably also indirectly, providing rich food resources - fungi and algae. The recognisable preference of *V. moulinsiana* for occupying indented parts in the upper blade surface indicate even more forcefully, in our opinion, these relations between the species and humidity. These "channels" are certainly more wind protected and more humid, and consequently more favourable for snails.

Vertigo moulinsiana was also distinguished by the percentage of juveniles, which was strikingly high in comparison with the other recorded Vertigo species. Other authors, especially Killeen (2003a,b), have also stressed the high abundance of juveniles, especially in the late summer and autumn. It seems that diverse percentages of juveniles in various Vertigo species are a consequence of their different life strategies. However, the species biology is generally little known in this group and therefore it is impossible to assess to what extent the high percentage of juveniles in V. moulinsiana is related to the occupied niche, i.e. existence in a relatively open space above the ground.

Vertigo antivertigo and V. pygmaea were rare in the fen. The former was scattered and occurred at sites of diverse ground moisture level, while the latter was concentrated in the driest parts of the fen (Fig. 3). The rare occurrence of these species in the study area is not explicable in the light of their known habitat preferences (Pokryszko, 1990), as they might have been abundant in this fen. Therefore, this rarity may reflect unknown mesoand microhabitat requirements of V. antivertigo and V. pygmaea or it may be related to the clear dominance of other co-occurring Vertigo species.

Vertigo angustior was also numerous in the temporarily disturbed part of the fen. It is not known whether agricultural activity influences the fen each year. However, on the photograph from September 2008 (available in Google Earth maps) a dry part of the fen had been mowed. V. angustior might have colonised this area during the two years (2009–2010) when mowing was discontinued or might have survived occasional late summer mowing. Irrespective of the possible explanation of the occurrence of V. angustior in this part of the fen, the species may not be very sensitive to some kinds of human impact and it may occur in some occasionally and/or extensively used habitats. Its congener, V. pygmaea, can even occur in habitats under strong anthropogenic pressure, such as gardens, pasture lands and railway embankments (Pokryszko, 1990). While such ecological plasticity does not conclusively characterise V. angustior, it is known from other studies that it may colonise relatively recently-created habitats (Killeen & Moorkens, 2011).

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Appendix 1 Number of recorded individuals of particular species at each sample site. Kind of samples: P – plant, T – thatch & litter, CS – control. Kind of sample site: D – disturbed, UND – undisturbed. Acronymes of species names: MOU – *Vertigo moulinsiana*, ANT – *Vertigo antivertigo*, ANG – *Vertigo angustior*, PYG – *Vertigo pygmaea*.

No. of sample site	Kind of sample	Kind of sample site	Number of individuals			
			MOU	ANT	ANG	PYG
1	T	D	_	1	2	_
2	T	D	_	_	4	_
3	T	D	_	_	4	_
4	T	D	_	_	4	_
5	T	D	_	_	5	_
6	T	D	_	_	3	_
7	T	UND	_	_	8	_
8	T	UND	_	_	_	4
9	T	UND	_	_	2	1
10	P	UND	_	_	3	_
11	T	UND	_	_	2	_
12	P	UND	1	_	_	_
13	T	UND	_	_	1	_
14	P	UND	_	_	_	_
15	T	UND	_	_	3	_
16	P	UND	_	_	_	_
17	P	UND	4	_	_	_

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No. of sample site	Kind of sample	Kind of sample site	Number of individuals			
			MOU	ANT	ANG	PYG
18	T	UND	_	_	_	_
19	P	UND	6	_	_	_
20	P	UND	9	_	_	_
21	T	UND	1	_	_	_
22	P	UND	10	_	_	_
23	P	UND	14	1	_	_
24	T	UND	3	_	_	_
25	P	UND	8	_	_	_
26	P	UND	12	_	_	_
27	T	UND	5	1	_	_
28	P	UND	8	1	_	_
29	T	UND	8	_	_	_
30	P	UND	6	1	_	_
31	P	UND	7	_	_	_
32	P	UND	6	_	_	_
33	T	UND	1	1	_	_
34	P	UND	28	1	_	_
1	CS	D	_	_	_	_
2	CS	D	_	_	_	_
Totally			137	7	41	5