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Using the Jolly-Seber model to characterise *Xerolenta obvia* (Gastropoda: Geomitridae) population

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Abstract

The terrestrial snail species *Xerolenta obvia* (Menke) has colonized dry, steppe-like habitats that have been created as a result of human activities in many countries outside the natural range of this species. In Latvia, this species was first recorded in 1989 in Liepāja. Observations in recent years in Liepāja have shown that snails from their initial introduction sites on the railway have also spread to the sand dune habitats within the city limits. Given that there are no snails in dune habitats that are biologically equivalent to *X. obvia*, this species is considered to be potentially invasive. As the distribution trends of this species in Liepāja indicate a possible threat to dry habitats in natural areas, detailed study of the species was conducted for the population of this species located in Dobele. Monitoring was performed from May 26 to August 5, 2019, carrying out 11 surveys with one week interval using the capture and re-capture method. The maximum recorded distance travelled by of one snail was 29.7 m; the calculated minimum estimated population density was 170 individuals and the maximum was 2004 individuals.

Key words: alien species, Dobele population, eastern heath snail, *Helicella candicans, Helicella obvia*, potentially invasive species.

Introduction

Xerolenta obvia (Menke), syn. *Helicella candicans* (L. Pfeiffer), *Helicella obvia* (Menke) is a relatively large snail species with a flattened white shell up to 22 mm in diameter, with brown bands on whorls. It is a xerophilous, thermophilous and heliophilous species, which inhabits steppe-like dry and open habitats and forms dense populations (Shileyko 1978; Barga-Więcławska 1990; Dvořák, Hory 2002; Hubenov 2007; Alexandrowicz, Alexandrowicz 2010; Zemoglyadchuk, Rabchuk 2014; Gural'-Sverlova, Gural' 2012; Balashov 2016; Kuźnik-Kowalska et al. 2017).

This species originated in the Pontic-Balkan region, but since the 17th century the species has become widespread in Central Europe (Alexandrowicz, Alexandrowicz 2010). Therefore, in some parts of Europe it is not possible to determine its natural range precisely. Presently it is known that the *X. obvia* is widespread in Europe (Austria, Belarus, Bulgaria, Czech Republic, France, Georgia, Germany, Greece, Hungary, Italy, Latvia, Lithuania, Moldova, Poland, Romania, Slovakia, Switzerland, Turkey and Ukraine) and Asia Minor; and in some countries the species is introduced (Shileyko 1978; Pilāte et al. 1994; Dedov 1998; Dvořák, Hory 2002; Gurskas 2002; Cholewa et al. 2003; Benke, Renker 2005; Lazaridou, Chatziioannou 2005; Hubenov 2007; Balashov et al. 2013; Gudžinskas et al. 2014; Forsyth et al. 2015; Balashov 2016). White-McLean (2012) mentions the species also for England and Ireland, but this report is probably a mistake, because the species is not confirmed in the British Isles, but a very similar species, *Helicella itala* (Linnaeus), occurs there (Cameron 2003).

Due to human activities, the species has been introduced also into Canada and United States in North America (Robinson, Slapcinsky 2004; Cowie et al. 2009; Wayne Grimm et al. 2009; White-McLean 2012; Foley et al. 2013; Forsyth et al. 2015). In the United States, *X. obvia* is recognised as a priority quarantine species (Cowie et al. 2009) and is listed by the Department of Agriculture as one of twelve invasive terrestrial snails (Cowie et al. 2009). In European countries outside its natural range, *X. obvia* has been found in Belarus, France, Germany, Latvia, Lithuania and Poland (Pilāte et al. 1994; Benke, Renker 2005; Alexandrowicz, Alexandrowicz 2010; Kuznecova, Skujienė 2011; Gudžinskas et al. 2014; Zemoglyadchuk, Rabchuk 2014; Forsyth et al. 2015; Zemoglyadchuk 2019). In Poland the species is alien in most of the country's territory, with the exception of the southern part, from which due to human activities snails have spread to other areas and are particularly found in synanthropic habitats (Alexandrowicz, Alexandrowicz 2010). Moreover, in Poland *X. obvia* is listed as an expansive species along with other terrestrial snails, such as *Cepaea nemoralis* (Linnaeus)

(Alexandrowicz, Alexandrowicz 2010). Dual distribution status is found also in Ukraine, where species is considered alien in Kiev and Zhitomir (Gural'-Sverlova, Gural' 2012; Gural'-Sverlova, Gleba 2015; Balashov 2016). In Germany, although *X. obvia* is an introduced species, it is considered that *X. obvia* is endangered in Saxony, where only two sites of this species are known (Benke, Renker 2005). In Lithuania, the first *X. obvia* specimen was found in Vilnius in 1993 (Gurskas 1997; 2002) in urban phytocoenoses (Kuznecova, Skujienė 2011), and was probably introduced with imported vegetables from Moldova or Ukraine (Gurskas 1997). Later, *X. obvia* was reported from another two localities in Lithuania, where large populations were observed (Gurskas 2009). In a recent publication it was mentioned that *X. obvia* is spreading, without explaining how the dispersal is occurring (Gurskas 2016). Gurskas (2016) also reported that *X. obvia* is an invasive species. Kuznecova, Skujienė (2011) reported that*X. obvia*, together with *Arianta arbustorum* (Linnaeus), are the dominant introduced pest species in Vilnius (Lithuania), which recently have spread rapidly.

Various man-made habitats are suitable for the species, where snails are found in industrial areas, abandoned quarries, gravel pits, factory and mine dumps, the ruins of abandoned buildings (including castles), roadsides, railways and vineyards, etc. (Barga-Więcławska 1990; Alexandrowicz, Alexandrowicz 2010; Kuznecova, Skujienė 2011; Foley et al. 2013; Horsák et al. 2013; Gudžinskas et al. 2014; Forsyth et al. 2015; Kuźnik-Kowalska et al. 2017).

In several countries, like in Belarus, Latvia, Lithuania, Poland and the United States, *X. obvia* has been found on railways, where even very large populations occur in Latvia and the United States (Robinson, Slapcinsky 2004; Zemoglyadchuk 2012; Gudžinskas et al. 2014; Zemoglyadchuk, Rabchuk 2014; Forsyth et al. 2015; Kuźnik-Kowalska et al. 2017; A. Stalažs, unpublished data). Robinson, Slapcinsky (2004) observed a large population found on a railway, which covered an area of seven hectares.

In Latvia *X. obvia* was first found in 1989, when snails were found in Liepaja on the railway (Pilāte et al. 1994). Due to lack of information on the origin of the species, *X. obvia* was erroneously included in the Red Data Book of Latvia (Spuris 1998). However, in Latvia the species is not native. It spreads due to human activities, and therefore it is not considered as endangered. Consequently, the species has been removed from the Red List of Latvian molluscs (Rudzīte et al. 2018). Currently, *X. obvia* is mostly found in Kurzeme and Zemgale regions (Rudzīte et al. 2010), where the species is known in many localities, most of which are located on railways (Gudžinskas et al. 2014).

Relatively recently, *X. obvia* was extensively studied in Greece (Lazaridou, Chatziioannou 2005), Belarus (Zemoglyadchuk 2019) and Poland (Kuźnik-Kowalska et al. 2017; Marzec et al. 2020). In Greece, two life cycles were observed for the species: a life cycle of one year and two years (Lazaridou, Chatziioannou 2005). In Belarus, observations suggested that *X. obvia* had only a one-year (annual) life cycle (Zemoglyadchuk 2019). In Poland, the *X. obvia* dominantly has an annual life cycle, and only 0.3% of the population is able to survive for two years (Marzec et al. 2020). Regardless of the life cycle longevity, snails die after laying eggs (Lazaridou, Chatziioannou 2005; Zemoglyadchuk 2019). The size of snail shells in different habitats can be affected by differences in local climate (Marzec et al. 2020).

So far, only the distribution of *X. obvia* has been studied in Latvia (Rudzīte et al. 2010; Gudžinskas et al. 2014; E. Dreijers, A. Stalažs and J. Stalažs, unpublished data), but the populations themselves have never been looked at in more detail. During these studies, it was found that the snails have begun to spread from railway habitats, where they were initially introduced in Liepāja city, to sand dune habitats within the city limits and other locations. Given this trend, this species may already be highly invasive in dune habitats in natural areas outside Liepāja. The same possibility exists in places where relatively dry habitats are found near railways, such as in open pine forests on inland sandy dunes and in dry meadows. The aim of the study was estimate population size of the species using the Jolly-Seber model for capture and re-capture data. This report provides an overview of the results of the study of the *X. obvia* population in Dobele (Zemgale region), data was collected from May 26 to August 5, 2019.

Materials and methods

Distribution of X. obvia *in Dobele*

The study was conducted in the summer of 2019 in Dobele (Latvia), in the area of the local population of *X. obvia* on the Jelgava-Liepāja railway line. During the study, the snails were marked, and the possible population size was calculated based on the obtained results.

In Dobele the species was first found in spring 2007. In this population snails were distributed in two separate places, between which they are not found in a zone less than a kilometre long. In a smaller area snails were found on the railway near the grain processing plant "Dobeles dzirnavnieks". In a larger area, snails occurred in the area from Dobele station in a north-western direction. Very few snails were found at the station itself (in 2019), and the snail population density has not increased here since the snails were first found in 2007. However, a large number of snails occurred starting from about 300 meters in the north-western direction from Dobele station. Here snails were mostly found on the railway and in the narrow grassland zone along it, from 56.629946 N, 23.282327 E to 56.634832 N, 23.274752 E. In the north-western direction, snails were found on the side of the street (Uzvaras iela, 56.639286 N, 23.266189 E), opposite a separate line of the railway that ends in a closed industrial area. As this area is closed for

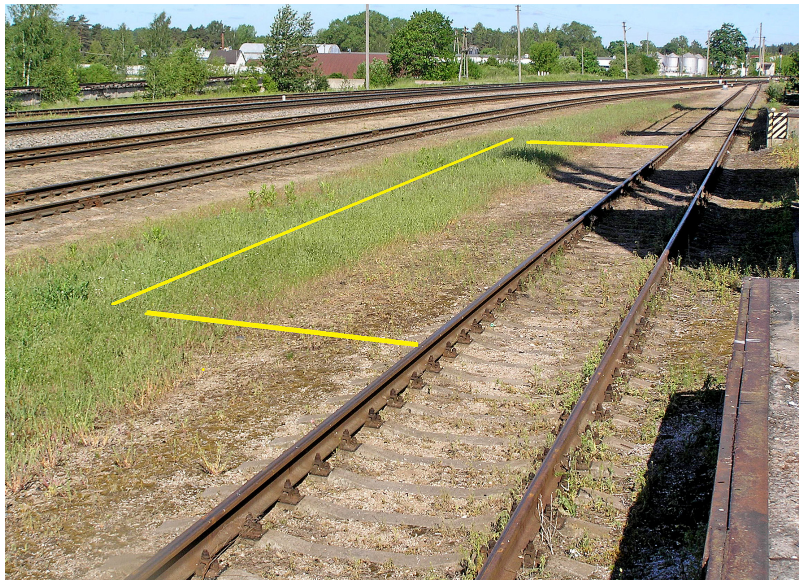

Fig. 1. Railway habitat overview and monitoring location (framed).

the public, survey was not carried out inside the property. In all places, snails were found on the railway and along the railway in low vegetation. Snails were practically not found in habitats with higher and too dense vegetation, except in some places where plants of Poaceae dominated, or the vegetation was not too dense. In general, moist habitats with dense vegetation continue along the railway, and snails ignore them. Therefore, their main population is directly along the railway and in a narrow area where habitats are drier.

Description of study plot

An inventory plot was set up for the study, with one end at 56.633361 N, 23.277306 E and other end at 56.633111 N, 23.277694 E. The plot area was 3.3 m wide and 33 m long along one rail (Fig. 1). This area was divided into 3.3 × 3.3 m squares, and 30 × 30 cm squares were marked in the middle of each larger square. Thus, there were a ten 30 × 30 cm squares with a total area of 9000 cm^2 in which the snails were counted and marked.

Vegetation characteristics

Vegetation was evaluated twice during the study. Vegetation was first described on May 26, 2019, the first monitoring day. The vegetation was described for the second time on June 18, 2019. Cover of plant species was estimated separately for each 3.3 × 3.3 m square using the following scale: ×, one to three, or some plants; 1, < 5%; 2, 5 to 25%; 3, 25 to 50%; 4, 50 to 75%; and 5, 75 to 100% (Table 1).

Between the first (May 26, 2019) and second monitoring day (June 3, 2019) when vegetation was evaluated, the railway operators had applied herbicides. Under the influence of herbicides, the plants along the rails died. This zone of herbicide application in some places reached marked 30 × 30 cm squares used for snail counting. In general, this herbicide-affected area noticeably differed in vegetation from the rest of the green area due to the herbicides used in previous years. Prior to the application of herbicides, on May 26 the vegetation was dominated by *Papaver rhoeas* and *Eschscholzia californica* with several other species. These two species were only present in the area treated with herbicides in previous years. After the application of herbicides, these plants decomposed rapidly, and later dead stalks of some plants remained in the area. Visual observations showed that there were very few snails in the area after herbicide application, and those occurred mainly on the rails or rail-holding bolts.

The marked snail counting 30 × 30 cm squares were located in vegetation of various composition. For example, in several squares, especially in square 1, the vegetation was very sparse. At the start of monitoring, the vegetation was much denser outside of around squares 9 and 10, as well as in square 10. As the vegetation season continued, the cover of plant species increased and more snails were observed on plants since about the middle of the monitoring period.

According to the railway maintenance requirements, before July 29, the lawn was cut in the area where young plants had sprouted in the herbicide-treated area. At the time of mowing, the cut narrow strip included nine of the ten 30 × 30 cm survey squares.

Snail marking

To ensure that individual snails are re-registered, they were all marked with an individual registration number. The number was written with a water-resistant marker and then covered with translucent nail polish. On each monitoring day a special record form was used to document snails. The following data was recorded: snails first found on that particular monitoring day; and snails which were re-captured. The individual number made it possible to

Table 1. Vegetation coverage in the study plot. ×, one to three, or some plants; 1, < 5%; 2, 5 to 25%; 3, 25 to 50%; 4, 50 to 75%; and 5, 75 to 100%

Plant species	Date	Number of each 3 × 3 m square									
		1	2	3	4	5	6	7	8	9	10
Achillea millefolium	May 25	–	–	×	–	–	–	–	–	–	–
	June 18	–	–	–	–	–	–	–	–	–	–
Anthemis tinctoria	May 25	–	×	×	–	×	×	–	–	×	×
	June 18	–	×	×	–	×	×	–	–	×	–
Artemisia sp.	May 25	–	–	–	–	–	–	–	–	–	–
	June 18	–	–	×	–	–	–	–	–	–	–
Barteroa incana	May 25	–	3	×	1	×	×	×	1	×	×
	June 18	×	4	2	3	2	2	2	2	1	1
Capsella bursa-pastoris	May 25	×	–	×	×	–	×	×	×	×	×
	June 18	–	×	–	–	–	–	–	–	×	×
Centaurea cyanus	May 25	–	–	–	–	–	–	–	–	–	–
	June 18	–	–	–	–	–	–	–	×	–	–
Echium vulgare	May 25	–	–	–	–	–	×	–	–	–	×
	June 18	–	–	–	–	–	×	–	–	–	×
Eschscholzia californica	May 25	–	–	–	–	–	×	×	×	×	×
	June 18	–	×	–	–	–	×	–	–	×	–
Geranium sp.	May 25	–	–	–	–	–	×	×	×	–	–
	June 18	–	–	–	–	×	–	×	×	×	–
Medicago spp.	May 25	1	×	×	1	×	×	×	×	×	×
	June 18	3	×	×	1	×	×	×	1	×	1
Oenothera biennis	May 25	×	–	×	×	×	×	–	–	×	×
	June 18	×	–	×	×	×	×	–	–	×	×
Papaver rhoeas	May 25	×	×	×	×	×	×	×	×	×	×
	June 18	–	–	–	–	–	–	–	×	×	×
Poaceae	May 25	3	3	3	3	3	3	3	3	3	3
	June 18	3	2	3	3	3	2	3	3	3	1
Potentilla argentea	May 25	–	–	–	–	–	–	×	–	–	–
	June 18	×	×	×	×	–	–	×	×	–	–
Potentilla reptans	May 25	×	–	–	–	–	–	–	–	–	–
	June 18	×	–	–	×	×	–	–	–	–	–
Rume× sp.	May 25	×	×	×	–	×	–	–	×	–	×
	June 18	×	×	1	×	×	×	×	×	×	×
Sedum acre	May 25	×	×	×	–	×	×	×	×	–	×
	June 18	×	×	×	×	×	×	×	×	×	×
Silene sp.	May 25	–	–	–	–	–	–	–	–	–	–
	June 18	–	–	–	–	–	×	×	×	×	×
Tara×acum officinale	May 25	–	–	–	–	–	–	–	–	–	×
	June 18	–	–	×	×	–	×	×	–	–	×
Tragopogon sp.	May 25	–	–	–	–	–	–	–	–	–	–
	June 18	–	×	×	–	–	–	–	–	–	–

recognise the day when a particular snail was marked for the first time, which was necessary for the calculation of population indicators. Only snails that were within 30 × 30 cm of the survey squares were marked for this study. Snail marking was performed every week 11 times on the following dates: May 26, 3, 10, 17 and June 25, 1, 9, 15, 22 and July 29 and August 5. Each time the snail marking was started around 9:00 in the morning. From the first to the fifth monitoring day, 24 snails could not be marked because of their very small size. These 24 snails were not used in the analysis.

Calculation of population parameters

To calculate snail population indicators, the Jolly-Seber model was used (Jolly 1965; Seber 1965), using formulas entered in MS Excel. The Jolly-Seber model uses capture-recapture data for open populations. Given that snail populations are variable and animals can migrate and

Table 2. Summary of captured and re-captured snail data (data matrix)

Last capture	Monitoring day										
	May 26	**June 3**	**June 10**	**June 17**	**June 25**	**July 1**	**July 9**	**July 15**	**July 22**	**July 29**	**August 5**
May 26		0	0	0	0	0	0	0	0	0	0
June 3			3	2	1	2	3	0	1	0	0
June 10				8	3	4	1	1	1	1	0
June 17					5	7	2	0	0	0	0
June 25						5	1	2	2	4	4
July 1							1	2	0	0	0
July 9								4	3	0	1
July 15									4	4	4
July 22										4	9
July 29											18
Total marked (*mt*)	0	0	3	10	9	18	8	9	11	13	36
Total unmarked (*ut*)	13	37	50	44	24	33	84	52	51	80	47
Total caught (*nt* = *mt* + *ut*)	13	37	53	54	33	51	92	61	62	93	83
Total released (*st*)	13	37	53	54	33	51	92	61	62	93	83

suffer mortality, the Jolly-Seber model is very suitable for population calculations, which makes the result more reliable (Nichols et al. 1981). For some groups of animals, age structure may be relevant in population calculations, requiring other calculation models (Jolly 1981). Given that the lifespan of *X. obvia* is short, generally annual (Lazaridou, Chatziioannou 2005; Zemoglyadchuk 2019; Marzec et al. 2020), the age structure is of no practical significance in the calculations. Therefore, it was assumed that in the case of *X. obvia*, the simple Jolly-Seber model is quite sufficient.

Results

A total of 549 snails were caught in the 30 × 30 cm squares, of which 525 snails were marked with an individual number (Table 2). Snails with too small size to enable marking were found from May 26 to July 1 (Fig. 2). The number of snails caught varied per each monitoring day (Fig. 2). At the time of capture, most of the snails were on plants and a small proportion was active and moving along the substrate. A total of 95 (18.1%) snails were re-captured, of which 19 (3.6%) were re-captured two or more times (Fig. 2). Of these, 76 were re-captured once, 14 re-captured twice, four re-captured three times and one re-captured four times. This demonstrates that in the general population of snails there was active movement, because only a small number of individuals stayed in one place between observation events. Seven snails were re-captured in different squares. Two of them were recaptured in adjacent squares, but the rest had moved a greater distances. One snail, which was marked in

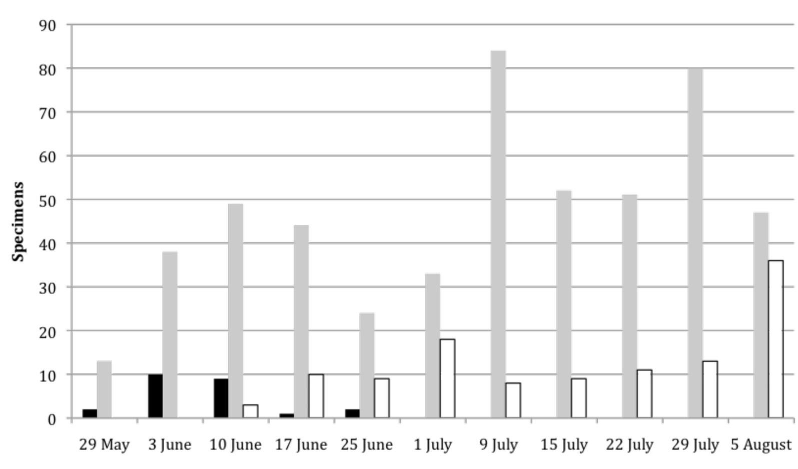

Fig.2. Un-marked, marked and re-captured *Xerolenta obvia* specimens for each monitoring day.

Table 3. Maximum travel distances recorded for re-captured snails

First capture		Re-capture		Days between first capture and re-capture	Distance of snail movement (m)
Square number	Date	Square number	Date		
5	June 3	3	July 9	36	6.6
2	June 10	3	June 25	15	3.3
4	June 10	3	June 25	15	3.3
7	June 17	9	July 9	22	6.6
7	June 25	10	July 29	34	9.9
5	July 1	3	July 15	14	6.6
1	July 9	10	August 5	27	29.7
9	July 9	7	July 22	13	6.6
7	July 22	10	August 5	14	9.9

square 1, was re-captured in square 10, indicating a travel distance of 29.7 m, estimated from centre of the squares (Table 3). However, the distances shown in Table 3 are only approximate, showing straight paths from point A to point B, rather than the actual distance travelled by the snails between the two monitoring days when snails were captured. In addition, some snails were re-captured in the same square where they were marked, but were missed on some observation dates. For example, one snail in square 10 was marked on 10 June and re-captured in the same square on 29 July. Another snail was marked in square 5 on June 3 but recaptured in square 3 on July 9 and again re-captured in the square 3 on July 22. In the cases of snails that have been re-captured after a longer period in the same square, there is a possibility that they have travelled little or that they have returned to the initial point of marking due to a coincidence.

All calculated population indicators are shown in Table 4. The estimated population size on July 9 was 2004 snails (Fig. 3), within the monitored area. As the total area of the squares where the snails were caught is 9000 cm^2, which is about 1 m^2, then it can be assumed that the calculation corresponds to an area of very close to 1 m^2.

There is no doubt that in this study, the snail population estimation was affected by grass mowing in nine of the ten survey squares. The decrease in the number of snails was already visible visually on July 29 and August 5, when the snails were in much smaller numbers in the squares where the grass was completely cut. It is not possible to say how the mowing of the grass in the nine squares affected the population size calculations, but it is possible that the calculated population size and the population dynamics curve (Fig. 3; Table 4) could have differed if such an external effect had not occurred. However, the effect of mowing is well seen in the baseline figures, which show that the sum of the number of snails in the first nine counting squares is less than the number of snails in the remaining 10th square alone (Fig. 4). The number of snails captured in square 10 on July 29 and August 5 increased, and the number of snails captured was higher than in the remaining nine squares. Comparing the last three monitoring days, which includes the day before mowing and the subsequent remaining two days, the snails caught in square 10 as a percentage of the total number of snails were as follows: 23.5% on July 22; 65.6% on July 29 and 72.3% on August 5. According to visual observations on the monitoring days, the vegetation cover

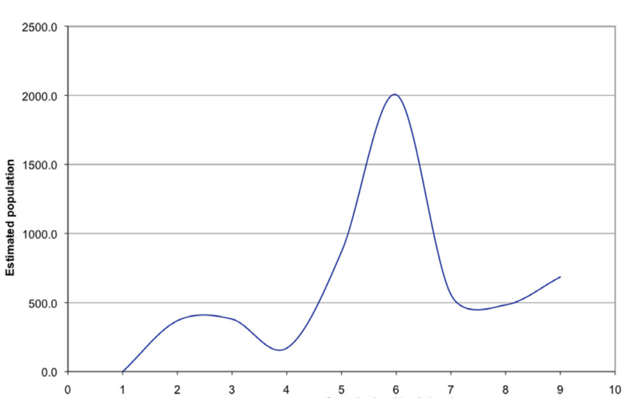

Fig.3. Dynamics of the estimated population size for *Xerolenta obvia* in Dobele population according to Jolly-Seber model statistics.

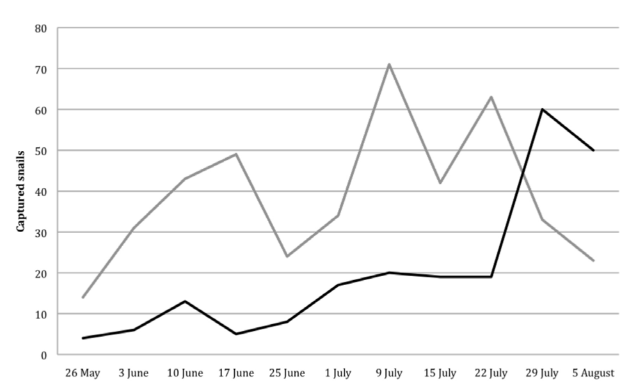

Fig.4. Total number of snails in squares 1 to 9 (gray line) compared to those caught in square 10 alone (black line). Before July 29, in the first nine squares had a completely cut grass.

Table 4. Estimated population characteristics, Jolly-Seber model statistics

No.	Sampling day Date	Marked proportion (*at*)	Marked population size (*Mt*)	Estimated population (*Nt*)	Survival probability (*ft*)	Number joining (*Bt*)
0	May 26	0.000	0.0	–	0.000	–
1	June 3	0.026	0.0	0.0	0.738	368.6
2	June 10	0.074	27.3	368.6	0.983	17.6
3	June 17	0.200	76.0	380.0	0.418	11.7
4	June 25	0.294	50.2	170.5	4.275	138.6
5	July 1	0.365	317.0	867.6	0.554	1523.8
6	July 9	0.097	194.0	2004.7	0.324	–91.1
7	July 15	0.161	90.1	558.5	0.648	121.4
8	July 22	0.190	92.0	483.0	0.714	340.5
9	July 29	0.149	102.1	685.2	–	–
10	August 5	0.440	–	–	–	–

had increased since the first half of July and a larger number of snails were observed on the plants. This vegetation also contained snails that were previously marked, but were outside the survey squares. Unfortunately, the chosen monitoring site did not have uniform vegetation, as cover was low in some survey squares. The richest vegetation was in the 10th square and next to the several other survey squares where snails were not counted. It can therefore be assumed that the number of snails could indeed reach 2000 per 1 m^2, but only in very ideal conditions when the snail habitat is not affected by human activity and when the climatic conditions are highly optimal. Vegetation cover had an effect on location of snails in the habitat. Given that the most optimal conditions were in the 10th accounting square, calculations for the last two observation days for this square, using the snails caught in this square at the end of July and in August, suggest that there were between 209 and 660 snails per m^2. Therefore, the snail density will never be homogeneous throughout the habitat due to differences in vegetation cover and density.

Snails were mostly found on Poaceae species, as well as *Barteroa incana* and *Medicago* spp., which have narrow leaves and a relatively sparse crown.

During the study, train freight cars were left next to the monitoring area for a few days. Walking along this train car set a specimen of *X. obvia* was observed on the side (top) of one car wheel. Before the last day of monitoring, the population of *X. obvia* in Jelgava was visited on August 3. This population is located on the same railway line. A large number of snails were observed at one Jelgava site (56.637207 N, 23.724687 E), shown in Fig. 5; the population density was much higher than at the Dobele monitoring site.

Discussion

The results obtained from a single-season study using the capture and recapture method showed potential application in further studies of *X. obvia* populations. However, more research should be done in the future in places with less human impact. This could also be ensured by agreeing with landowners or maintainers that no specific activities, such as grass mowing, are carried out at the monitoring site. Given that the species is widespread in synanthropic conditions and in artificial habitats, such conditions would be needed for studies to better understand the potential of *X. obvia*

Fig.5. *Xerolenta obvia* in one of the populations in Jelgava (August 3, 2019, 56.637207 N, 23.724687 E).

to affect natural habitats, where no adverse human effects are observed. Future studies should also clarify the best plot size for snail marking, which could be 50 × 50 cm instead of the 30 × 30 cm size squares used in this study. However, it would not be advisable to place larger individual plots in denser vegetation, because, as it was difficult to mark snails in the 30 × 30 cm squares when they were too many. It may be necessary to increase the number of survey squares to cover as many different vegetation plots as possible in the same habitat.

The result of the calculation was obtained when the maximum number of snails was calculated as 2004 individuals in an area of 1 m^2, which could be true under suitable vegetation cover. However, this is an artificially calculated population size, and in reality the population size should be estimated by averaging over variable vegetation cover and density. However, as indicated above, the method for population calculations would still need to be tested elsewhere, as well as in several seasons. In the United States, it was estimated that *X. obvia* could reach one million or even more specimens per acre in six locations (Foley et al. 2013), which could be 247 or more snails per 1 m^2. Our calculations for square 1 gave estimates of 209 to 660 snails m^{-2}.

These observations show that under optimal conditions there may be even more snails, thus exceeding 200 individuals per 1 m^2, observed in the United States. Given that the studt was only carried out for one season, final conclusions for Latvian conditions cannot yet be obtained. However, the existing data show that, at least in the Dobele population, the maximum number of snails definitely varies up to 200 individuals per 1 m^2. Nevertheless, it was concluded that population densities of *X. obvia* fluctuate from year to year and may vary from study site to study site, which may vary on average from 22 to 84 individuals per 1 m^2 (Lazaridou, Chatziioannou 2005). They also found that population growth occurred in July and August. Although our study was completed on August 5, population growth was well visible from mid-July. This was especially evident from the data of the 10th survey square, where no grass was mowed during the study period.

However, even with the smallest estimated number of snails at 170 individuals per 1 m^2, and as observed in different other populations in Latvia, the population densities of *X. obvia* are several times higher than that of any other species. According to observations, another alien species (*A. arbustorum*) ranks second in Latvia, reaching a high population density in wetter habitats (A. Stalažs, unpublished data). Until now, the populations of *X. obvia* in Latvia have been found mainly in urban areas, mostly on railways. In these areas, the species cannot be considered invasive because these habitats are either not natural or too heavily influenced by human activities. However, the information gathered so far and the results of the studies suggest that *X. obvia* may become a highly invasive species if snails will reach dry natural habitats.

The need for vegetation for snails was very well observed during this study. The monitoring area was dominated by plants with a sharper crown, as well as species that do not tend to form dense vegetation. The existence of certain plant species forming denser group-like communities in a particular habitat certainly does not prevent *X. obvia* from occupying the this habitat. The negative effects of grass mowing and after herbicide applicationo on *X. obvia* were also clearly visible during this monitoring in Dobele. Disappearance of snails was also observed in Jelgava, near Jelgava station, where there were many snails in a narrow zone along the railway in 2018, but in 2019 after regular mowing, only a few living specimens could be found in some places at electrical poles (A. Stalažs, unpublished data).

X. obvia is known to occur on plants during the summer diapause, in a period when the activity of snails is low (Forsyth et al. 2015; Zemoglyadchuk 2015). During this time they are located on plants, or on object above the topsoil. The observations showed that the snails were on rails and rail bolts in places where herbicides were applied. The rails were the only objects on which the snails could take refuge during the dormant period, since only dead plant stems in the rail area immediately after the application of herbicides. This means that snails still need objects, albeit dead plants (Forsyth et al. 2015), above the ground during their dormant period, because during this period they were never observed on the soil. It is most

Table 5. Snail fauna of dry habitats (forests, meadows and dunes) in Latvia: an overview

Species	Family	Reference	Remarks
Aegopinella pura (Alder, 1830)	Gastrodontidae	Dreijers, Stalažs 2000	
Arianta arbustorum (Linnaeus)	Helicidae	Dreijers, Stalažs 2000	Alien and invasive species. Mainly in the vicinity of populated areas
Arion fuscus (O. F. Müller)	Arionidae	Dreijers, Stalažs 2000	
Arion vulgaris (Moquin-Tandon)	Arionidae	Stalažs et al. unpublished data	Alien and highly invasive species. Mainly in the vicinity of populated areas
Carychium minimum O. F. Müller	Ellobiidae	Dreijers, Stalažs 2000	
Cepaea hortensis (O. F. Müller)	Helicidae	Dreijers, Stalažs 2000	

Table 5. *continued*

Species	Family	Reference	Remarks
Cepaea nemoralis (Linnaeus)	Helicidae	Dreijers, Stalažs 2000	Alien species. Mainly in the vicinity of populated areas
Clausilia bidentata (Strøm)	Clausiliidae	Dreijers, Stalažs 2000	
Cochlicopa lubrica (O. F. Müller)	Cochlicopidae	Pilāte 1997; 2007b; Dreijers, Stalažs 2000	
Cochlicopa lubricella (Porro)	Cochlicopidae	Pilāte 1997; 2003, 2007b; Dreijers, Stalažs 2000	In some localities dominant species
Cochlodina laminata (Montagu)	Clausiliidae	Dreijers, Stalažs 2000	
Columella aspera Waldén	Truncatellinidae	Pilāte 1997; 2007b; Dreijers, Stalažs 2000	
Columella edentula (Draparnaud)	Truncatellinidae	Pilāte 1997	
Deroceras reticulatum (O. F. Müller)	Agriolimacidae	Stalažs et al. unpublished data	
Deroceras sturanyi (Simroth)	Agriolimacidae	Stalažs et al. unpublished data	
Discus ruderatus (W. Hartmann)	Discidae	Pilāte 2007b	
Euconulus fulvus (O. F. Müller)	Euconulidae	Pilāte 1997; 2007b; Dreijers, Stalažs 2000	
Fruticicola fruticum (O. F. Müller)	Camaenidae	Dreijers, Stalažs 2000	
Helicigona lapicida (Linnaeus)	Helicidae	Pilāte 2007a; Kursīte 2014	
Krynickillus melanocephalus Kaleniczenko	Agriolimacidae	Stalažs et al. unpublished data	Alien and highly invasive species. Now also widespread in natural habitats
Limacus maculatus (Kaleniczenko)	Limacidae	Stalažs, Dreijers, data about habitats unpublished	Alien species. Dry gardens, railway edge in the territory of Riga city
Limax maximus Linnaeus	Limacidae	Stalažs et al. unpublished data	Alien species. Found in sand dune habitats in Liepāja and Pāvilosta
Perpolita hammonis (Strøm)	Gastrodontidae	Pilāte 1997; 2007b; Dreijers, Stalažs 2000	
Punctum pygmaeum (Draparnaud)	Punctidae	Dreijers, Stalažs 2000; Pilāte 2007b	
Pupilla muscorum (Linnaeus)	Pupillidae	Pilāte 2003; 2007b; Dreijers, Stalažs 2000	In some localities dominant species
Succinea putris (Linnaeus)	Succineidae	Pilāte 1997	
Succinella oblonga (Draparnaud)	Succineidae	Dreijers, Stalažs 2000	
Trochulus hispidus (Linnaeus)	Hygromiidae	Dreijers, Stalažs 2000	
Truncatellina cylindrica (A. Férussac)	Truncatellinidae	Stalažs 2000	
Vallonia costata (O. F. Müller)	Valloniidae	Dreijers, Stalažs 2000; Pilāte 2007b	
Vallonia excentrica Sterki	Valloniidae	Pilāte 2003; 2007b; Dreijers, Stalažs 2000	In some localities dominant species
Vallonia pulchella (O. F. Müller	Valloniidae	Pilāte 2003; 2007b; Dreijers, Stalažs 2000	
Vertigo lilljeborgi (Westerlund)	Vertiginidae	Pilāte 2007b	
Vertigo pusilla O. F. Müller	Vertiginidae	Pilāte 1997; Dreijers, Stalažs 2000	
Vertigo pygmaea (Draparnaud)	Vertiginidae	Dreijers, Stalažs 2000; Pilāte 2007b	
Vertigo substriata (Jeffreys)	Vertiginidae	Dreijers, Stalažs 2000	
Vitrea crystallina (O. F. Müller)	Pristilomatidae	Dreijers, Stalažs 2000	
Vitrina pellucida (O. F. Müller)	Vitrinidae	Pilāte 2003; 2007b; Dreijers, Stalažs 2000	
Xerolenta obvia (Menke)	Geomitridae	Pilāte et al. 1994; this study	In semi-wild dry habitats within the city of Liepaja
Zonitoides nitidus (O. F. Müller)	Gastrodontidae	Dreijers, Stalažs 2000	

likely because the snails on the soil would be exposed to too much solar radiation and could overheat. Escaping from extreme soil surface temperatures by climbing on plants is characteristic to various species inhabiting dry and open habitats (Schweizer et al. 2019). Overheating of snails on the ground is one of the methods by which similar species are restricted in Australia by deliberately shaking them on the hot ground (Kempster, Charwat 2003). In terms of temperature, in warmer regions *X. obvia* has a larger shell (Marzec et al. 2020).

Given that this species inhabits mainly dry and open habitats (Shileyko 1978; Dvořák, Hory 2002; Hubenov 2007; Alexandrowicz, Alexandrowicz 2010; Zemoglyadchuk, Rabchuk 2014; Gural'-Sverlova, Gural' 2012; Balashov 2016; Kuźnik-Kowalska et al. 2017), where the temperature may be high in summer, this is probably why the species has adapted to be at rest on the surface of various objects.

The literature also indicates that *X. obvia* needs low vegetation (Zemoglyadchuk 2012) and inhabits grass communities such as *Poetum compressae* (Skujienė, Vaivilavičius 2001) in Lithuania. Such plant communities can be found both in the population of *X. obvia* in Dobele and in populations found elsewhere in Latvia. In addition, observations in Dobele showed that wetter habitats as well as denser plant communities are not suitable for the snails, what confirms observations made in other countries. Given that the railways are artificially designed to be dry, such artificial tracks form narrow corridors between wet and even marshy habitats, as well as between wooded and shrub areas that are not suitable habitats for the species. This describes the snail habitat in Dobele, where they live in a narrow area on and along the railway. However, as already mentioned in the introduction, in Liepāja the species has spread to wider areas outside the railway areas, because there the railway tracks border with many dry and open habitats, which are typical for the Baltic Sea coast. Nevertheless, the characteristics of the vegetation on the railways in Dobele are similar to places where there are many more dry habitats along the railways. Therefore, the results of the observations can be interpreted for different habitats.

Unfortunately, there are a small number of publications on the fauna of Latvian dry habitats. However, it was possible to obtain information on species found in suitable habitats of *X. obvia* from several publications issued in last decades. A total of 40 species of snails have been found in dry and open habitats (meadows, dunes and pine forests) in Latvia, of which 32 are native and eight are introduced, and three of these alien species are highly invasive (see references in Table 5). Pilāte (2007b) studied grey dune fauna in six places in Latvia and found 14 species of snails, all of which were small in size, and of these species, *Cochlicopa lubricella* (Porro), *Vallonia excentrica* Sterki and *Pupilla muscorum* (Linnaeus) were predominant. Of these species, *P. muscorum* was predominant and accounted for about 60% of the total snail collection in the grey dunes of Ziemupe, where *C. lubricella* accounted for only 3%, and *V. excentrica* for 12% (Pilāte 2003). These studies suggest that dune habitats are more dominated by *P. muscorum*, while other species vary in dominance. According to Pilāte (2007b), the 14 species found were of average density of 24.7 individuals per 1 m^2. As shown in an overview in Table 5, in dry and open habitats most species are small in size, but larger species may also be present in these habitats. However, none of the major species in these habitats has been found at high density, as is typical of *X. obvia*. This suggests that *X. obvia* will spread into natural open habitats, where the overall structure of snail species communities will rapidly change. As can be seen in places where *X. obvia* is already present, the microclimate and environmental conditions in natural habitats could also change, as a large number of *X. obvia* empty shells will accumulate in these habitats. Without changes in the environmental microclimate, competition between native species and *X. obvia* will be expected. As can be seen in the overview in Table 5, non-native species (*A. arbustorum, Arion vulgaris, C. nemoralis, Deroceras sturanyi, Krynickillus melanocephalus, Limacus maculatus, Limax maximus*), which are not typical for the respective habitats, already now occur in dry and open habitats. Species like *C. nemoralis, D. sturanyi, L. maculatus, L. maximus*, are found in these habitats only locally in and around human settlements, and the rapid spread of these species in the wild is unknown. Unfortunately, the same cannot be said for other species, in particular *A. vulgaris* and *K. melanocephalus*, which are characterised by rapid spread in wild habitats.

X. obvia is one of the pioneer species capable of surviving in disturbed habitats where the soil is disturbed as well as which is exposed to high temperatures. *X. obvia* is an euryecologic species capable of tolerating isolated, dry or moderately moist habitats (Barga-Więcławska 1990). The species needs plants and other over soil-surface objects where to take refuge. Usually, man-made and severely disturbed habitats always have places (islands) where such snails can take refuge. As a result, the snails are able to survive and gradually take over a new area where ruderal vegetation can develop smoothly, which is usually sparse and suited to the needs of *X. obvia*. Such conditions also exist in habitats on railways. Given that *X. obvia* may be a pioneer species in such warm and open habitats, this suggests the potential of this potentially invasive species to become a highly invasive in the future.

In view of the mentioned above, it is necessary to carry out further studies on the possible effects of *X. obvia* on other species, as well as to monitor the species in order to reduce its potential for further spread within the country.

The capture and re-capture method not only makes it possible to calculate the estimated population density or other population parameters, but also makes it possible to obtain additional information on the marked animals, such as the movement distances of the particular individuals. The distance recorded in this study of more than 29 m indicates that *X. obvia* can move relatively long distances in its habitat. Further research in the future, using the capture and re-capture method in snail movement studies, could provide more information on possible population expansion rates.

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