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Demographic and spatial structure at the stage of expansion in the populations of some alien land snails in Belgorod city (Central Russian Upland)

V.V. ADAMOVA*, P.A. UKRAINSKIY, O.V. KRYMSKAYA

Belgorod National Research University, 85, Pobedy St., Belgorod, 308015, RUSSIAN FEDERATION

*Corresponding author; E-mail: valeriavladislavna@gmail.com

ABSTRACT. Studying of the demographic characteristics of populations of alien species at the stage of expansion makes it possible to assess their invasive potential. Field studies of alien terrestrial gastropods *Xeropicta derbentina* (Gastropoda, Stylommatophora, Hygromiidae), *Brephulopsis cylindrica* (Gastropoda, Stylommatophora, Enidae) and *Harmozica ravergiensis* (Gastropoda, Stylommatophora, Hygromiidae) have been carried out in Belgorod city, the southern part of the Central Russian Upland (Russia). All studied species are native to the Black Sea region and the Caucasus; in the southern part of the Central Russian Upland, they have been registered over the past ten years. The population density, demographic structure, and spatial structure have been analyzed for three years of observations (2017, 2019, 2020). During this period, the changes in the population density have been noted for all studied species. The most pronounced changes have been observed in *X. derbentina*, whose population density has significantly decreased, and the spatial structure has changed from clustered type to random distribution. In addition, the age structure of *X. derbentina* population had a pronounced change at the beginning of the snail activity season of 2020.

The expansion of the other two invaders, *B. cylindrica* and *H. ravergiensis*, is proved as more successful. At the same time, *H. ravergiensis* is distributed throughout the city. This species has stable population density and random type of spatial population structure on most sites. *B. cylindrica* has the highest population density: in 2020, it has reached 406 ind./m^2 on average, with the maximum of 1215 ind./m^2. Meantime, the species keeps the clustered spatial structure, which is explained by both high population density and adaptation to the arid conditions of its natural range.

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Демографическая и пространственная структура популяций некоторых чужеродных видов наземных моллюсков на территории Белгорода (Среднерусская возвышенность)

В.В. АДАМОВА*, П.А. УКРАИНСКИЙ, О.В. КРЫМСКАЯ

Белгородский национальный исследовательский университет, ул. Победы 85, Белгород, 308015, РОССИЙСКАЯ ФЕДЕРАЦИЯ

* *Автор-корреспондент; E-mail: valeriavladislavna@gmail.com*

РЕЗЮМЕ. Изучение демографических особенностей популяций чужеродных видов на стадии экспансии позволяет оценить их инвазивный потенциал. Полевые исследования чужеродных наземных гастропод *Xeropicta derbentina* (Gastropoda, Stylommatophora, Hygromiidae), *Brephulopsis cylindrica* (Gastropoda, Stylommatophora, Enidae) и *Harmozica ravergiensis* (Gastropoda, Stylommatophora, Hygromiidae) были проведены на территории юга Среднерусской возвышенности в Белгороде (Россия). Все виды нативны для Причерноморья и Кавказа, а на юге Среднерусской возвышенности их первые находки были отмечены в течение последних десяти лет. Анализ динамики плотности популяций, их демографической структуры и пространственной организации был выполнен на основании данных за три года наблюдений (2017, 2019, 2020). За этот период отмечены изменения плотности популяции у всех исследуемых видов. Наибольшие изменения наблюдались у *X. derbentina*, плотность популяции которой значимо снизилась, а пространственная организация сменилась с агрегированной на случайную. Кроме того, популяция *X. derbentina* продемонстрировала смену возрастной структуры в начале сезона активности в 2020 году.

Экспансия двух других вселенцев оказалась более успешной. При этом *H. ravergiensis* распространена по всей территории города и имеет достаточно стабильные значения плотности популяции и случайный тип пространственного распределения на большинстве исследуемых участков. *B. cylindrica*

имеет наиболее высокую плотность популяции: в 2020 году средняя плотность достигла 406 особей на метр квадратный, а максимальное значение достигло 1215 особи на метр квадратный за этот же год. При этом вид сохраняет агрегированную пространственную структуру, что объясняется не только высокой плотностью, но и адаптацией к аридным условиям естественного ареала.

Introduction

Invasive species are perfect object for studying the population processes at early stages of the species expansion at new territory or water area. A complex of biotic and abiotic factors, as well as the adaptive potential of the non-indigenous species, preconditions the success of the invasion [Mooney, Cleland, 2001; Lee, Gelembiuk, 2008]. Invasive process has a number of certain stages, and the population structure undergoes certain change at each stage [Facon *et al.*, 2006; Kolar, Lodge, 2001]. Any stage in this process may be fatal for an alien species. Since many invaders are eliminated at the initial stage of the invasive process, it is important to assess the features of a new alien population [Williamson, Fitter, 1996]. This allows identifying the characteristics of the species that make them successful invaders. In this regard, the population density and age structure are the key parameters of the invader population. Changes in the population density affect reproduction rate and, ultimately, the expansion process [Yoshida *et al.*, 2013; Neiman *et al.*, 2013; Strayer, Malcom, 2006; Zachar, Neiman, 2013]. The population density of invasive species contributes to its ecological impact during expansion [Jackson et al., 2015].

In this article, we present a study of the demographic and spatial structure of populations of nonindigenous gastropods *Xeropicta derbentina* (Krynicki, 1836), *Brephulopsis cylindrica* (Menke, 1828), and *Harmozica ravergiensis* (Férussac, 1835). The native range of *X. derbentina* covers the eastern Mediterranean region, the Black Sea region, Caucasus and Anatolia [Schileyko, 1978; Aubry *et al*., 2005]. *B. cylindrica* is native of Crimean Peninsula [Puzanov, 1925]. The spread of this species along the Northern Black Sea coast in the 20th century is associated with the introduction of the species [Schileyko, 1984]. *H. ravergiensis* spread widely but sporadically over the North and South Caucasus [Schileyko, 1978].

However, they have been spreading in recent decades northwards and northwestwards the native range. *X. derbentina* is the most widely distributed alien terrestrial gastropod among these three species, characterized by the widest native range [Schileyko, 1978]. Its populations have been found in different regions of Ukraine and in several countries of Western Europe [Aubry *et al*., 2005; De Mattia, 2007; De Mattia, Pešić, 2014; Gural-Sverlova, Gural, 2017; Holyoak, Seddon, 1985; Kiss *et al.*, 2005; Kramarenko, Sverlova, 2001]. The Crimean snail *B. cylindrica* is another non-indigenous species. Its populations have been registered in Ukraine in the northern Black Sea region, the Donetsk Ridge, the Dnieper Lowland, and the Podolian Upland; some authors reported on the finds of this species in Belarus [Kramarenko, Sverlova, 2001; Gural-Sverlova, 2018; Balashov *et al.*, 2018a; Rabchuk, Zemoglyadchuk, 2011].

We have the least information about the third invader, the Caucasian land snail *H. ravergiensis*. This species has been found in Ukraine, namely, on the Podolian Upland, the Donetsk Upland, and the Dnieper Lowland [Balashov, 2016; Balashov *et al.*, 2018b]. In addition, *H. ravergiensis* has been registered in the Moscow and Tver Regions (the East European Plain) [Schikov, 2016]. In the southern part of the Central Russian Upland (Belgorod, Russia), the populations of this species have been found from 2002 to 2014 [Snegin, Prisniy, 2008; Snegin, Adamova, 2016; Adamova *et al.*, 2019].

Two of the studied species, *X. derbentina* and *B. cylindrica*, are xerophilic and typical for open steppe habitats [Gural-Sverlova, 2018; Cameron *et al*., 2013]. On the Crimean Peninsula, these species coexist on the same territory, and their populations are quite numerous here [Kramarenko, 1997; Popov, Dragomoschenko, 1997]. Outside the native range, the populations of these species have the same demographic characteristics. A variety of features may contribute to their successful expansion. For instance, *X. derbentina* can "switch" the life cycle, characterized by high ecological plasticity outside the natural range [Kiss *et al.*, 2005]. Alien populations of *B. cylindrica,* inhabiting the Dnieper Upland, are characterized by the same features of demographic and spatial structure comparing to those in native range [Kramarenko *et al*., 2014]. In addition, the spatial organization of this sub-population of *B. cylindrica* depends greatly on the composition and properties of soil [Zhukov *et al*., 2019]. Populations of *X. derbentina* are numerous outside the natural range and are characterized by a plasticity of the life cycle [Kiss *et al*., 2005].

The population characteristics of the third alien species, *H. ravergiensis*, have not yet been practically studied. According to our previous studies, *H. ravergiensis* successfully spread on the territory of the city of Belgorod, inhabiting various biotopes [Snegin, Adamova, 2016].

We selected these species as the object of our study due to the fact that the territory of the south of the Central Russian Upland is a forest-steppe and, therefore, steppe alien snails can affect native ecosystems.

Searching for the dependence of the dynamics of the demographic process in the invader population

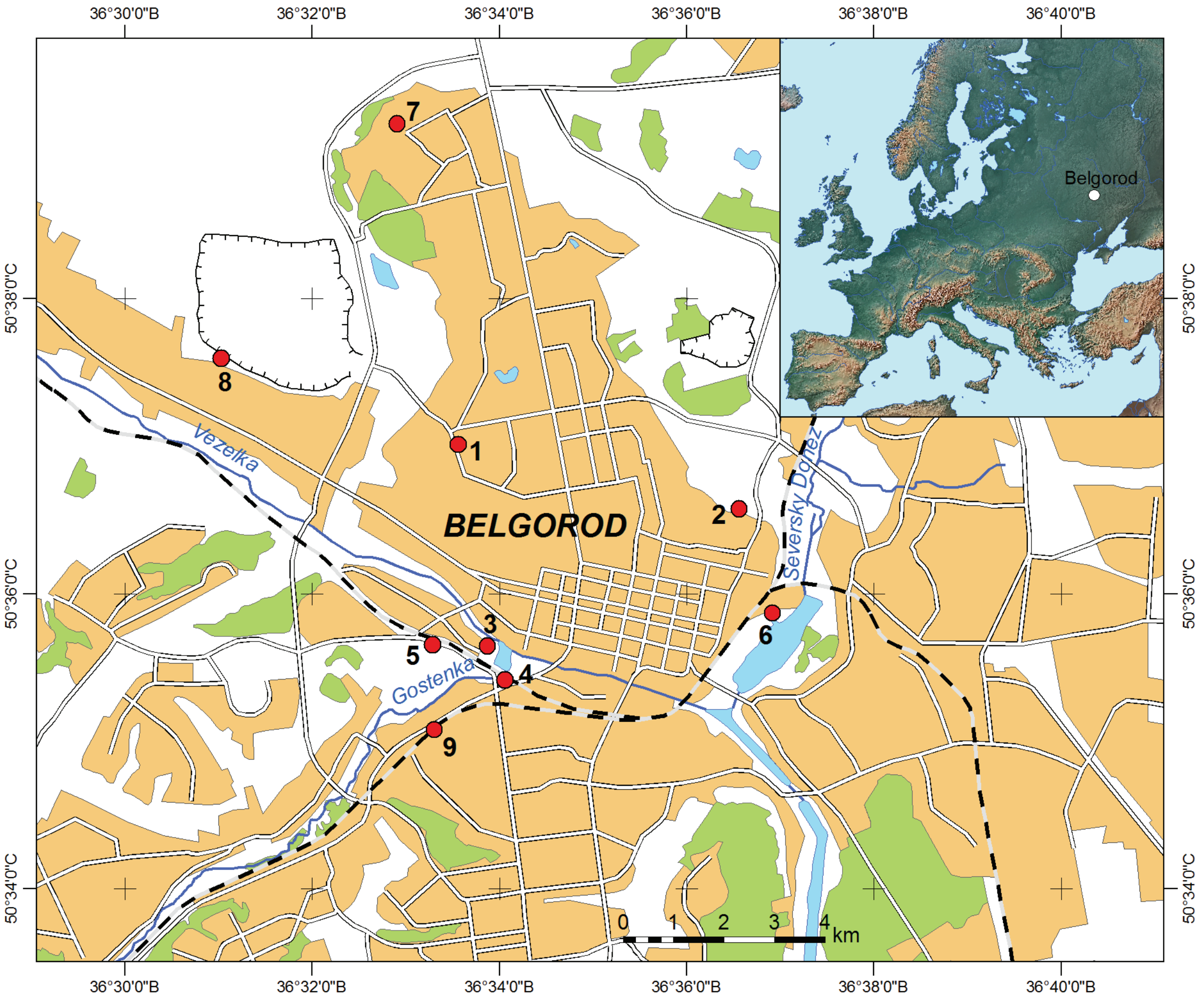

FIG. 1. Map of study sites.

РИС. 1. Карта размещения исследуемых участков.

on the climatic parameters in a new habitat is one of the key issues. Despite the significant role of the reproductive potential of an alien species, the environmental factors cannot be ignored when studying the structure of its population during the process of expansion. The influence of climatic changes on the fate of invasive species is known for many plants, animals, and their pathogens [Hulme, 2017; Simberloff, 2000]. This factor affects all stages of invasion, from dispersal of the species to its expansion and adaptation to new conditions. Invasive species have often pronounced response to climate change [Sax *et al.*, 2007; Hulme, 2005], reflected in their morphological and genetic characteristics [Chown *et al.*, 2015; Albarrán-Mélzer *et al.*, 2020; Kelly, 2019]. Climatic changes, in particular, global warming, can often favor the colonization of new territories by invasive molluscs; some gastropods and bivalves are considered to be listed in the top 100 of the world's worst invasive alien species [Luque *et al.*, 2014]. Climatic changes contribute to worldwide invasion of *Achatina fulica* (Férussac, 1821) and *Pomacea canaliculata* (Lamarck, 1822) [Rekha Sarma *et al.*, 2015; Lei *et al.*, 2017]. In general perspective, global climate change will favor an increase in the number of invasive species in several regions of the world, in particular, in the northeastern Europe [Bellard *et al.*, 2013].

The study aims to assess the demographic structure and spatial organization of alien populations of *X. derbentina*, *B. cylindrica*, and *H.ravergiensis* at the northernmost margin of the expanding range.

Material and methods

Study site

All studied sites were located on the territory of Belgorod city (Belgorod Region, Russia, Fig. 1). Populations of *B.cylindrica* and *X. derbentina* were located in the open area with steppe vegetation near a chalk mining (50°37'35.90"N, 36°31'01.33"E).

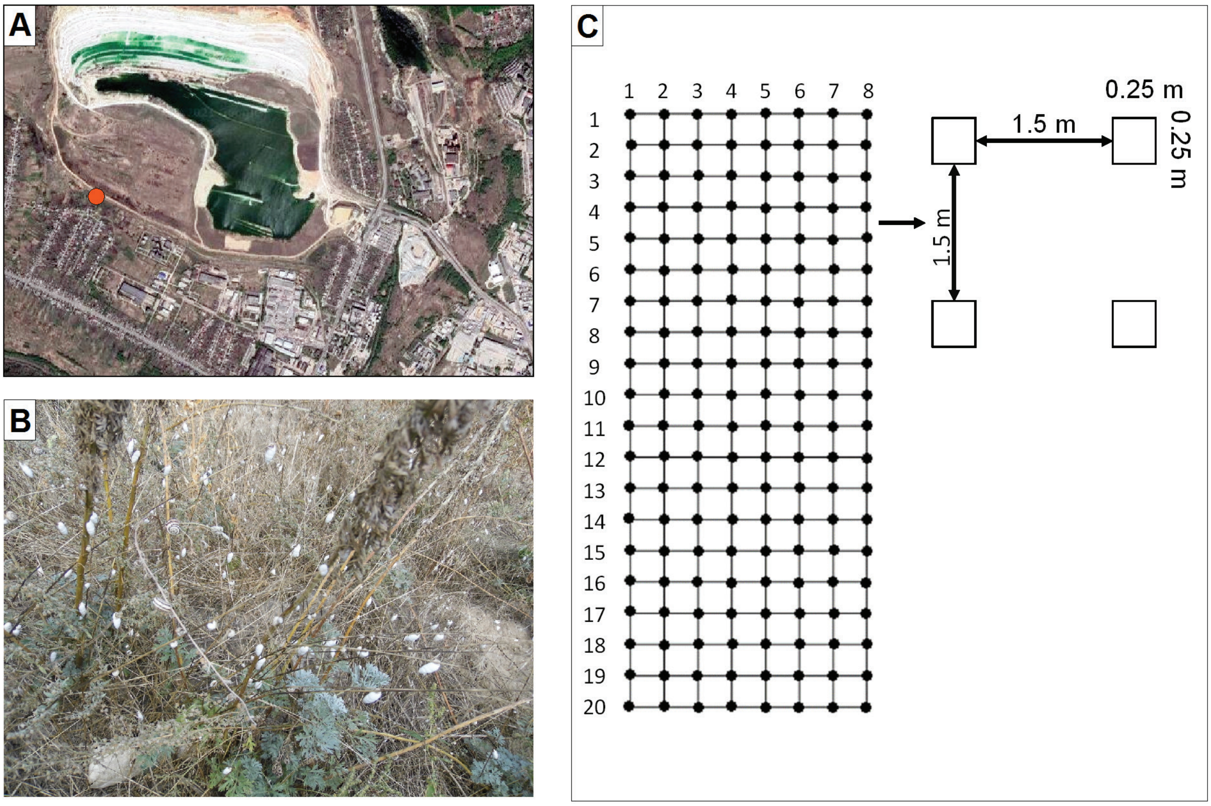

FIG. 2. Scheme of plots in a regular grid. **A.** Study site. **B.** *Brephulopsis cylindrica* and *Xeropicta derbentina* in the field. **C.** Scheme of plots in a regular grid.

РИС. 2. Регулярная сетка площадок. **A.** Расположение исследуемого участка. **B.** *Brephulopsis cylindrica* и *Xeropicta derbentina* в месте обитания. **C.** Схема регулярной сетки площадок.

H. ravergiensis has already spread throughout the territory of Belgorod city, so nine sites were inspected during our study. All sites were located on anthropogenically modified areas, but they differed in environmental characteristics (Table 1, Fig. 1).

Sampling and analyses

B. cylindrica and *X. derbentina* were collected from May through September (the period of snail activity) in 2017, 2019, and 2020. *H. ravergiensis* was sampled in the same months in 2019 and 2020.

The quadrat sampling method was applied. The population density of *H. ravergiensis* was assessed at each of the nine sites, the specimens were counted totally at 20 random plots (each of 0.25 m^2). A regular grid of 8 transects was set to study the population density and spatial distribution of *B.cylindrica* and *X. derbentina* populations, each transect had 20 plots (each of 0.25 m^2). The center of each plot was located in a 1.5-m distance from the center of neighboring plots (Fig. 2). This sampling scheme followed that proposed by Kramarenko et al. [2014]. After sam-

Table 1. Brief description of the sampling sites.

Таблица 1. Краткое описание участков отбора проб.

No.	Sampling site	Coordinates
1	Wasteland with ruderal vegetation near industrial zone	50°37’00.71”N 36°33’33.40”E
2	Industrial zone near a chalky slope	50°36’34.62”N 36°36’33.79”E
3	Floodplain of the Vezelka River near a suburban settlement	50°35’38.70”N 36°33’52.36”E
4	Shaded site in the floodplain of the Vezelka River along railway tracks	50°35’25.00”N 36°34’03.54”E
5	Maple woods near the Botanical Garden of Belgorod State University	50°35’39.32”N 36°33’17.07”E
6	Floodplain of the Severskii Donets River near the railway station	50°35’52.13”N 36°36’55.03”E
7	Maple woods in a suburban settlement	50°39’11.4”N 36°32’53.30”E
8	An open area with steppe vegetation between a suburban settlement and a chalk quarry	50°37’35.90”N 36°31’01.33”E
9	Wasteland with ruderal vegetation along the railroad tracks	50°35’15.60”N 36°33’48.20”E

Table 2. Average monthly temperature (°C) during the study period and the climate normal for the study area. Data from Belgorod Center for Hydrometeorology and Environmental Monitoring.

Таблица 2. Средняя месячная температура (°C) в исследуемый период и климатическая норма для изучаемой территории по данным Белгородского центра по гидрометеорологии и мониторингу окружающей среды.

Month	Year			Climate normal
	2017	2019	2020	
January	-6.8	-6.1	1.8	-7.6
February	-5.1	-2.1	-0.5	-6.0
March	3.8	2.2	5.6	-0.9
April	8.3	10	7.7	8.4
May	13.9	16.9	12.7	15.1
June	18.3	22.4	12.3	18.6
July	20.5	19.6	21.6	20.1
August	21.8	19.8	20.0	18.8
September	15.4	15.3	17.5	13.4
October	6.7	10	6.8	6.9
November	1.1	2.4	5.4	0.4
December	1.8	0.6	2.5	-4.9

pling and accounting all the snails were taken back to the same site.

In 2019 and 2020, the population density of *X. derbentina* was also studied in a 45-m distance from the regular grid, in addition to the sampling performed on the regular grid. Here, the number of *X. derbentina* was counted similarly to the scheme applied for *H. ravergiensis* (20 random plots, each of 0.25 m^2). These additional sampling was performed since there was a decrease of *X. derbentina* abundance along the regular grid, where the abundance of *B. cylindrica* was higher in 2019 and 2020.

In order to study the age structure of population, *B. cylindrica* and *X. derbentina* were subdivided into two age classes: juveniles and adults (snails with a fully developed lip on the shell for *B. cylindrica* and snails with more than 5 shell whorls for *X. derbentina*). *H. ravergiensis* specimens were subdivided into three age classes: juveniles (up to 3.5 shell whorls), subadults (more than 3.5 shell whorls), and adult (snails with a fully developed lip).

Statistical analysis

The Kruskal-Wallis test [Kruskal, Wallis, 1952] was applied to analyze the differences in the population density of *B. cylindrica* and *X. derbentina* between the study years for each month. Since the abundance of *H. ravergiensis* was counted at different sites, the differences between these sites by year were estimated using two-way analysis of variance (two-way ANOVA) [Fisher, 1925; Fujikoshi, 1993]. A two-way ANOVA was performed using a linear model –function (lm) in R, where the sampling year and the site were variances. The data were evaluated for each month separately.

To compare the proportion of age classes by year, a post hoc analysis for Pearson's chi-squared test was applied [Beasley, Schumacker, 1995].

Since all the studied species are native to the warmer climatic regions (Crimea and the Caucasus), the Spearman correlation coefficient [Zar, 1972] was applied to study the dependence of the population density on the average temperatures of the respective month. We used average monthly temperatures for the cold period of the year and climate normal for the study area to interpret population density differences over the years. Average monthly data were the courtesy of the Belgorod Center for Hydrometeorology and Environmental Monitoring (Table 2). Climate normal for Belgorod city are indicated for the averaging period from 1961 to 1990 according to the data obtained by the Hydrometeorological Research Center of the Russian Federation (https://meteoinfo.ru/).

Bivariate spatial cross-correlation between *B.cylindrica* and *X. derbentina* population density was calculated using local Moran's-I (LISA), following Chen [2015] to test the hypothesis of species interaction.

The global Moran's index [Anselin, 1995] was applied to estimate the spatial structure of *B.cylindrica* and *X. derbentina* populations. The Morisita index [Morisita, 1959, 1962] was used for the analysis of spatial patterns of *H.ravergiensis* population on each site separately. The estimation of the spatial structure of the *H.ravergiensis* was summarized for 5 months for 2019 and for 2020.

Most of the calculations were performed in R with standard package, in addition, packages "stats", "spatialEco" and "chisq.post.hoc" were used [R Core Team, 2020]. Data processing on the spatial structure of populations was carried out using the ArcGIS 10.2 program.

Results

Over three years of observations, the population density of alien species changed, but remained rather high for *B. cylindrica.* and *H. ravergiensis*. Statistically significant differences between the years were revealed for *B. cylindrica* and *X. derbentina*, as evidenced by the Kruskal-Wallis test (Table 3, 4). Two-way ANOVA test shows the difference between the years in *H. ravergiensis* population only in May and June, but there is a statistically significant differences between sites (Table 5).

B. cylindrica had the highest population density (Table 6), reaching the maximum (average for 160 sites) of 1920 ind./m^2 (September 2017), 1168 ind./m^2 (June 2019), and 1215 ind./m^2 (May 2020). The average abundance was also quite high. The high-

Table 3. Results of Kruskal-Wallis test for *Brephulopsis cylindrica* population density between three years/

Таблица 3. Результаты однофакторного дисперсионного анализа Крускала-Уоллиса для плотности популяции *Brephulopsis cylindrica* за три года

Month	chi-squared	df	p-value
May	104.62	2	< 0.001
June	40.076	2	< 0.001
July	116.27	2	< 0.001
August	161.90	2	< 0.001
September	7.836	2	0.019

Table 4. Results of Kruskal-Wallis test for *Xeropicta derbentina* population density between three years.

Таблица 4. Результаты однофакторного дисперсионного анализа Крускала-Уоллиса для плотности популяции *Xeropicta derbentina* за три года.

Month	Chi-squared	Df	p-value
May	13.462	2	0.001
June	15.588	2	< 0.001
July	7.9683	2	0.019
August	32.409	2	< 0.001
September	25.181	2	< 0.001

est average population density of *B. cylindrica* was recorded in 2020. In some months, its abundance exceeded two- or threefold that observed in previous years. In addition, a higher density of juveniles was noted within the whole study period in 2020, except for September (Table 7, Fig. 3). In all years of observation, the same dynamics of change in the age classes of *B. cylindrica* was observed, when the share of juveniles was the highest at the beginning of the activity season; the opposite pattern was observed by the end of the season, when adult specimens prevailed.

Another alien species, *X. derbentina*, was not so successful in the new habitats. In 2017, the population density of this snail was quite high in the area of regular grid, where the density of *B. cylindrica* was also high (Table 8). However, in 2019, the abundance of *X. derbentina* decreased by almost 10 times within this area. In 2020, only a few specimens of this species have been found within the regular grid. At the same time, the population density of *X. derbentina* remained quite high and in 2019 reached its maximum in September in a 45-m distance from the regular grid (Table 9). In 2020, the abundance of *X. derbentina* also decreased in this area, but the highest values were observed in July-August. The ratio of age classes varied during the season of snail activity and slightly differed from year to year (Table 7, Fig. 4). Taking into account a one-year life cycle of this species in its natural range, its age structure attracted much interest in May 2020. In previous years, the proportion of adults who survived the winter did not exceed a few percent at the beginning of the season of snail activity, but in May 2020, 52.94% of the population of *X. derbentina* were adult molluscs.

The population density of the third alien species, *H. ravergiensis*, differed between years, in May-June 2020 the population density decreased in comparison with the previous year (Table 5, 10). Since this gastropod is the most widely dispersed alien mollusc species throughout the city of Belgorod, we analyzed its population at nine sites (Table 1). In all

Table 5. Two-way ANOVA results for *H. ravergiensis* population density between two years and sites.

Таблица 5. Результаты двухфакторного дисперсионного анализа для популяции *H. ravergiensis* между годами и участками.

Month	Source of variation	Df	Sum Sq	Mean Sq	F	p-value
May	site	8	22218	2777.2	17.626	< 0.001
	year	1	5259	5259.4	33.379	< 0.001
	site:year	8	3112	389.0	2.467	0.013
June	site	8	34654	4331.7	15.052	< 0.001
	year	1	17	17.3	0.060	0.806
	site:year	8	11181	1397.6	4.857	< 0.001
July	site	8	104846	13105.8	35.364	< 0.001
	year	1	0	0.0	0.000	1.000
	site:year	8	0	0.0	0.000	1.000
August	site	8	63283	7910.4	16.301	< 0.001
	year	1	0	0.0	0.000	1.000
	site:year	8	0	0.0	0.000	1.000
September	site	8	41444	5180.4	27.183	< 0.001
	year	1	0	0.0	0.000	1.000
	site:year	8	0	0.0	0.000	1.000

Table 6. Population density (ind./m^2) of *Brephulopsis cylindrica* for three years.

Таблица 6. Плотность популяции (особей/м^2) *Brephulopsis cylindrica* за три года.

Year		Month				
		May	June	July	Aug	Sept
2017	D_{mean}±SE	250±19	149±16	86±12	79±7	145±20
	Me	168	56	16	48	64
	D_{max}	1104	1040	720	480	1920
2019	D_{mean}±SE	158±17	204±18	183±17	139±16	129±14
	Me	48	128	80	64	64
	D_{max}	976	1168	1120	912	864
2020	D_{mean}±SE	300±15	323±19	390±18	300±15	132±11
	Me	308	300	385	323	77
	D_{max}	1215	1077	1092	969	831

In all months D_{min}=0

Table 7. The distribution of different age groups in the populations of *Brephulopsis cylindrica* and *Xeropicta derbentina*.

Таблица 7. Распределение частот отдельных возрастных групп в популяции *Brephulopsis cylindrica* и *Xeropicta derbentina.*

species	year	Month									
		May		June		July		August		September	
		J	A	J	A	J	A	J	A	J	A
B. cylindrica	2017	0.93	0.07	0.88	0.12	0.64*	0.36*	0.52	0.48	0.76*	0.24*
	2019	0.84	0.16	0.88	0.12	0.75	0.25	0.75*	0.25*	0.71*	0.29*
	2020	0.82	0.18	0.86	0.14	0.80	0.20	0.52	0.48	0.33*	0.67*
X. derbentina	2017	0.96	0.04	0.98	0.02	0.95	0.05	0.70	0.30	0.50	0.50
	2019	0.96	0.04	0.91	0.09	0.97	0.03	0.78*	0.22*	0.80*	0.20*
	2020	0.47*	0.53*	0.94	0.06	0.96	0.04	0.34*	0.66*	0.36	0.64

J - juvenile snails, A - adult snails. Statistically significant differences between years according to the chi-square test with post hoc analysis (p-value <0.05) are indicated by *

Table 8. Population density (ind./m^2) of *X. derbentina* in the area of regular grid for three years.

Таблица 8. Плотность популяции (особей/м^2) *X. derbentina* на площадках, расположенных по регулярной сетке за три года.

Year		Month				
		May	June	July	Aug	Sept
2017	D_{mean}±SE	41±4	136±13	111±12	24±3	28±4
	Me	32	80	48	16	0
	D_{min}	0	0	0	0	0
	D_{max}	320	800	736	288	432
2019	D_{mean}±SE	4±1	3±1	3±1	3±1	3±1
	Me	0	0	0	0	0
	D_{min}	0	0	0	0	0
	D_{max}	64	96	48	48	112
2020	D_{mean}±SE	0±0	0±0	0±0	0±0	0±0
	Me	0	0	0	0	0
	D_{min}	0	0	0	0	0
	D_{max}	1	3	4	3	2

In all months D_{min}=0

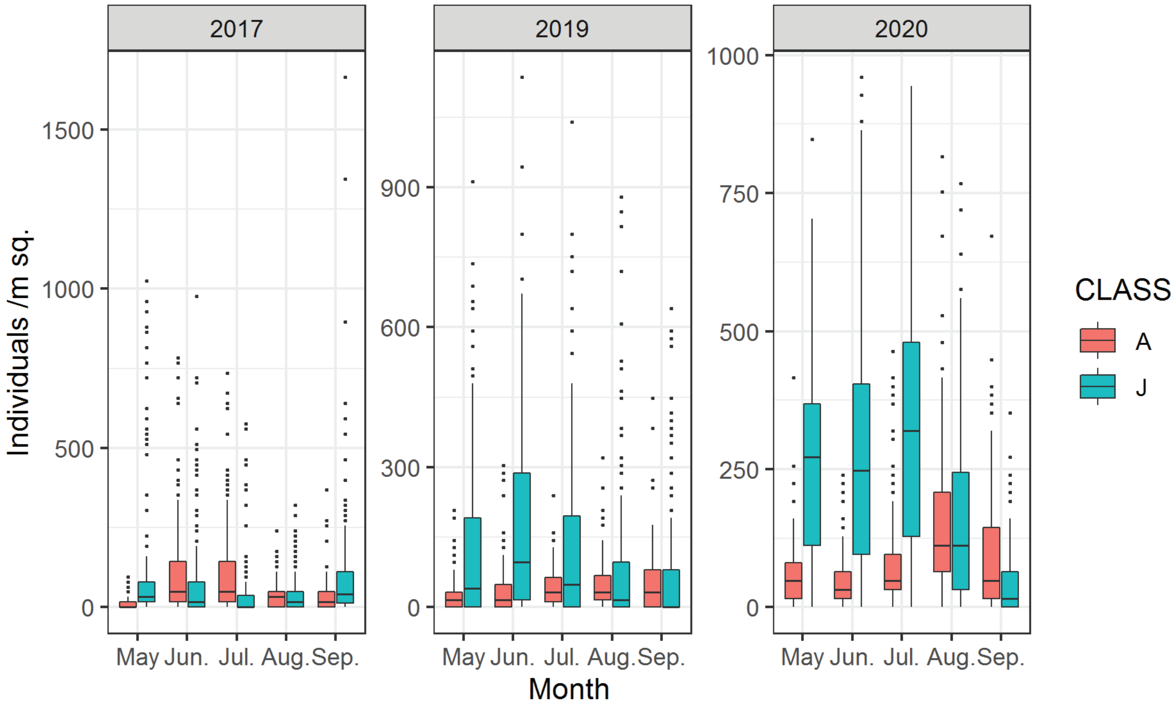

FIG. 3. Boxplots for estimating the density of different age classes in the *Brephulopsis cylindrica* population in warm months of 2017, 2019, and 2020 for 160 test plots. Adult snails are represented by red boxes; juvenile snails are represented by blue boxes.

РИС. 3. Боксплоты для оценок плотности различных возрастных классов в популяции *Brephulopsis cylindrica* в разные теплые месяцы 2017, 2019 и 2020 гг. для 160 пробных площадок. Взрослые особи показаны красным цветом, ювенильные особи показаны голубым цветом.

cases, there were significant differences between the sites. The population density of *H. ravergiensis* was the highest at the site no. 2, notable for its chalky outcrops, compared to other sites in May and June for both years of observation. Significant differences were also found for the sites nos. 4 and 6, but these statistical differences were found only in May. We present the primary data of population density for all sites, evidencing that the *H. ravergiensis* population had stable density values and reached its maximum in August before the beginning of reproductive season (Table 10).

The ratio of size-age classes in *H. ravergiensis* population in most sites did not change in 2020 or differed in any of the months of observation in some sites (Table 11). There were differences in the share of juvenile and subadult specimens in the site 2 in May and June. Also in the site 1, the proportion of adults was different in 2020 from July to September.

Dominance of adult specimens in the population was observed for all three studied species in August and September, during the reproductive period.

The population density of *H. ravergiensis* (Spearman's test: rho =0.072, p=0.002) depended on the average temperature of the month of observation. However, no significant dependence was found for

Table 9. Population density (ind./m^2) of *Xeropicta derbentina* at a distance of 45 m from the regular grid for two years.

Таблица 9. Плотность популяции (особей/м^2) *Xeropicta derbentina* на расстоянии 45 м от регулярной сетки за два года.

Year		Month				
		May	June	July	Aug	Sept
2019	D_{mean}±SE	22±3	32±6	26±3	54±6	62±7
	Me	16	24	0	56	48
	D_{max}	48	112	48	112	128
2020	D_{mean}±SE	14±5	18±3	38±6	32±6	11±2
	Me	0	16	32	32	16
	D_{max}	64	48	96	128	32

In all months D_{min}=0

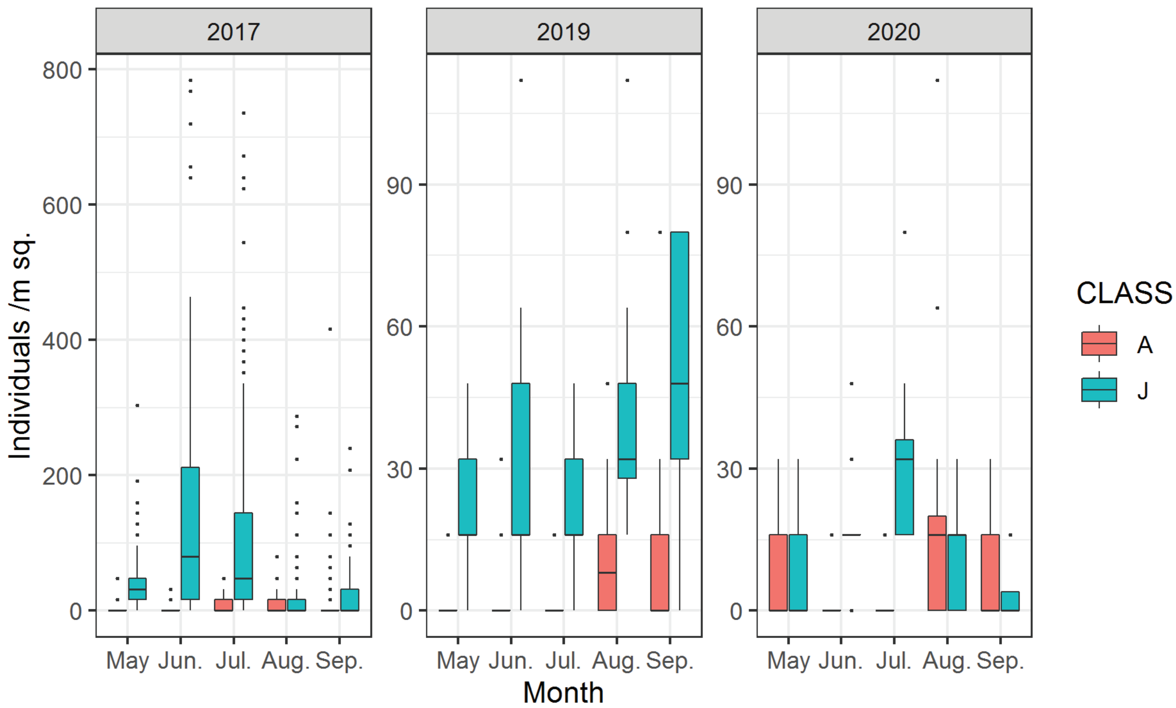

FIG. 4. Boxplots for estimating the density of different age classes in the *Xeropicta derbentina* population in warm months of 2017, 2019, and 2020 for 160 test plots. Adult snails are represented by red boxes; juvenile snails are represented by blue boxes.

РИС. 4. Боксплоты для оценок плотности различных возрастных классов в популяции *Xeropicta derbentina* в разные теплые месяцы 2017, 2019 и 2020 гг. для 160 пробных площадок. Взрослые особи показаны красным цветом, ювенильные особи показаны голубым цветом.

X. derbentina (Spearman's test: rho =0.001, p=0.983) and *B. cylindrica* (Spearman's test: rho =-0.011, p=0.598).

During three years of observations, the spatial structure of populations of alien xerophilic species changed as well (Table 12). In 2017, both xerophilous mollusc species had a predominantly aggregated spatial distribution. Only at the end of the season, *X. derbentina* was characterized by a random distribution.

In 2019 and 2020, there were both a decrease in the abundance of *X. derbentina* and the change in the spatial structure of its population. During the period of activity, snails of this species were randomly distributed over the site.

In most sites the spatial distribution of *H. ravergiensis* population was random both in 2019 and 2020 (Table 13). Only in the site 2 it was aggregated. It is noteworthy that at the same site there was a maximum population density in both years.

Discussion

Several conclusions can be drawn from the analysis of our results. First, the population density was quite high for *B. cylindrica*. We suppose that the increase in population density of *B. cylindrica* may suppress locally the other two invaders. Nowadays, *H. ravergiensis* is distributed throughout the territory of the whole city of Belgorod, although it is not the most numerous invader. Therefore, we observe two successful alien species with different strategies.

The change in the proportion of age classes during the season represents the life cycle of the studied snail species. This is consistent with known data for these species inhabiting the native range in the northern Black Sea region [Kramarenko, 1997; Popov, Dragomoschenko, 1997]. A significant number of adults in the population of *X. derbentina* in May 2020 suggests that this species is able to switch to a two-year life cycle, as it has been observed for other invasive populations of this species [Kiss *et al.*, 2005].

The spatial structure of xerophilous non-indigenous gastropods is similar to that observed in other parts of their ranges [Kramarenko *et al.*, 2014; Zhukov *et al.*, 2019]. Aggregated spatial distribution is one of the adaptations to the habitat of steppe biotopes under arid conditions. At the same time, as the population density of *X. derbentina* decreases, the spatial organization of the population changes as well. The spatial distribution of *H. ravergiensis* in the most sites was random, except the site with the maximum population density, where it was aggregated.

The air temperature affects the abundance of *H. ravergiensis*.

Table 10. Population density (ind./m²) of *Harmozica ravergiensis* for two years.

Таблица 10. Плотность популяции (особей/м²) *Harmozica ravergiensis* за два года.

Site	*D*	Month				
		May	June	July	August	September
2019						
1	D_{mean}±SE	25±4	26±4	26±5	18±3	25±6
	Me	24	32	16	16	16
	D_{max}	48	64	80	48	96
2	D_{mean}±SE	31±4	35±5	25±5	52±11	53±7
	Me	32	32	16	48	56
	D_{max}	80	96	96	224	128
3	D_{mean}±SE	19±3	20±4	13±2	14±2	10±2
	Me	16	16	16	16	16
	D_{max}	48	48	32	32	16
4	D_{mean}±SE	11±2	18±4	24±4	14±3	10±3
	Me	16	16	16	16	16
	D_{max}	32	80	64	48	32
5	D_{mean}±SE	18±2	24±4	22±3	18±3	17±3
	Me	16	16	16	16	16
	D_{max}	32	48	48	48	48
6	D_{mean}±SE	21±3	27±5	19±3	22±3	12±2
	Me	16	16	16	16	16
	D_{max}	48	80	64	48	32
7	D_{mean}±SE	10±2	16±3	20±5	18±3	14±3
	Me	16	16	16	16	16
	D_{max}	32	48	80	48	80
8	D_{mean}±SE	9±2	15±2	6±2	7±2	4±2
	Me	8	16	0	0	0
	D_{max}	32	48	32	16	32
9	D_{mean}±SE	19±3	22±5	18±4	10±2	8±2
	Me	16	16	16	16	8
	D_{max}	48	96	80	32	16
total for all sites	D_{mean}±SE	**18±1**	**23±1**	**19±1**	**19±2**	**17±2**
	Me	16	16	16	16	16
	D_{max}	80	96	96	224	128
2020						
1	D_{mean}±SE	12±2	16±3	35±4	41±5	20±3
	Me	16	16	32	40	16
	D_{max}	32	32	80	96	48
2	D_{mean}±SE	33±6	56±6	63±10	51±7	41±4
	Me	16	64	48	48	48
	D_{max}	96	112	160	128	800

Table 10. Continued.

Таблица 10. Продолжение.

Site	D	Month				
		May	June	July	August	September
3	D_{mean}±SE	8±2	21±3	14±2	18±2	11±2
	Me	0	16	16	16	16
	D_{max}	32	48	32	48	32
4	D_{mean}±SE	10±2	11±2	10±2	26±6	17±2
	Me	16	16	16	16	16
	D_{max}	32	32	32	112	32
5	D_{mean}±SE	5±2	19±3	18±3	23±3	22±3
	Me	0	16	16	16	16
	D_{max}	32	48	48	48	64
6	D_{mean}±SE	20±3	34±4	34±4	33±8	27±5
	Me	16	32	32	16	16
	D_{max}	48	80	64	176	80
7	D_{mean}±SE	0±0	30±4	15±3	16±3	10±2
	Me	0	24	16	16	8
	D_{max}	0	80	48	48	32
8	D_{mean}±SE	2±1	5±2	7±2	8±2	1±1
	Me	0	0	0	8	0
	D_{max}	16	16	16	16	16
9	D_{mean}±SE	4±2	9±2	10±2	12±3	17±4
	Me	0	8	8	16	16
	D_{max}	16	32	32	64	48
total for all sites	D_{mean}±SE	**11±1**	**22±2**	**23±2**	**25±2**	**18±1**
	Me	0	16	16	16	16
	D_{max}	96	112	160	176	80

In all months D_{min}=0

Population size and age structure

A high population density of non-indigenous species is expected at the first stages of its expansion. Population abundance often grows at the stage of the introduction of alien species into a new territory and further colonization [Crooks *et al.*, 1999]. In this case, species with certain traits, primarily reproductive, are considered more successful invaders [Sakai *et al.*, 2001]. Among invasive molluscs, such examples are freshwater species *Potamopyrgus antipodarum* (Gray, 1843) and *Physa acuta* (Draparnaud, 1805) [Levri, Lively, 1996; Neiman *et al.*, 2013; Saha *et al.*, 2019]. The species, characterized by fast population growth rate and thus reaching extremely high population density, may even overcome the negative effects of interspecific interactions [Alonso, Castro-Díez, 2012; Verhaegen *et al.*, 2021]. However, one should consider that populations of many invasive species may also have boom-bust dynamics [Strayer *et al.*, 2017; Wasson et *al.*, 2020]. Therefore, the high population density or absolute abundance do not necessarily guarantee the further success of the invasion.

Many species of snails and slugs have seasonal fluctuations in population density [Cameron, Pokryszko, 2005]. Changes in the proportion of different age groups during the season represent the life cycle of these species. As a rule, in all studied species juveniles predominate at the beginning of the season, and the proportion of adults increases by the end of the season. The abundance peaks are in June-July, followed by a slight decline. For *B.*

Table 11. The distribution of different age groups in the populations of *Harmozica ravergiensis.*

Таблица 11. Распределение частот отдельных возрастных групп в популяции *Harmozica ravergiensis.*

year	site	Month														
		May			June			July			August			Sept.		
		J	SA	A	J	SA	A	J	SA	A	J	SA	A	J	SA	A
2019	1	0.23	0.52	0.23	0.22	0.50	0.28	0.39	0.48	0.12	0.26	0.52	0.22	0.29	0.39	0.33
	2	0.05	0.62	0.33	0.32	0.37	0.32	0	0.35	0.65	0.05	0.09	0.86	0	0.21	0.79
	3	0.08	0.46	0.46	0.16	0.48	0.36	0	0.69	0.31	0	0.53	0.47	0	0.31	0.69
	4	0.21	0.34	0.45	0.30	0.30	0.39	0.10	0.17	0.73	0.11	0.33	0.56	0	0.5	0.5
	5	0.14	0.65	0.23	0.23	0.60	0.17	0.04	0.59	0.37	0	0.45	0.55	0	0.38	0.62
	6	0.12	0.54	0.35	0.18	0.53	0.29	0.13	0.75	0.13	0.30	0.56	0.15	0.33	0.40	0.27
	7	0.08	0.77	0.15	0.40	0.35	0.25	0	0.52	0.48	0.04	0.22	0.74	0	0.35	0.65
	8	0.18	0.82	0	0.32	0.53	0.16	0	0.5	0.5	0.11	0.11	0.78	0	0.40	0.60
	9	0.17	0.67	0.17	0.15	0.64	0.21	0.14	0.32	0.56	0.08	0.25	0.67	0	0.40	0.60
2020	1	0.67	0.33	0	0.05	0.85	0.10	0.09	0.64	0.27	0	0.06	0.94	0	0	1.00
	2	0.63	0.15	0.22	0.08	0.82	0.10	0.01	0.84	0.15	0.02	0.17	0.81	0	0.12	0.88
	3	0.40	0.40	0.20	0.03	0.77	0.2	0.11	0.83	0.06	0.04	0.70	0.26	0	0.21	0.79
	4	0.38	0.31	0.31	0	1.00	0	0.08	0.62	0.31	0	0.38	0.63	0.10	0.43	0.48
	5	0.83	0.17	0	0.21	0.75	0.04	0.09	0.70	0.22	0.03	0.24	0.72	0	0.26	0.74
	6	0.16	0.48	0.36	0.10	0.74	0.17	0.21	0.57	0.21	0.05	0.22	0.73	0.06	0.23	0.71
	7	0	0	0	0.11	0.70	0.19	0.05	0.79	0.16	0	0.25	0.75	0	0	1.00
	8	0	1.00	0	0	0.83	0.17	0	0.56	0.44	0	0.20	0.80	0	0	1.00
	9	0.80	0.20	0	0.09	0.91	0	0	1.00	0	0	0.33	0.67	0	0.38	0.62

J - juvenile snails, SA subadult snails, A - adult snails. Statistically significant differences between years according to the chi-square test with post hoc analysis (p-value <0.05) are indicated by gray color

cylindrica, similar dynamics have been observed in other populations of this species and of another species of this genus, *Brephulopsis bidens* (Krynicki, 1833) [Livshits, 1983; Kramarenko, 1997]. According to these authors, the decrease in snail abundance in the middle of summer is due to the mass death of juveniles in the hottest summer months. Moreover, *B. cylindrica* buries in the soil during the period with maximum temperatures. This adaptive behavior is typical for some other steppe and desert snails, for example, *Sphincterochila boissieri* (Charpentier, 1847) [Schmidt-Nielsen *et al.*, 1971].

The dynamics of *X. derbentina* population was quite pronounced during the observation period. In 2017 the size of this population was comparable to the other studied populations of this species [Popov, Dragomoschenko, 1997; Kiss *et al.*, 2005, Aubry et *al.*, 2005]. Then, in 2019 and especially in 2020, the population size greatly decreased (Table 4). The proportion of adult specimens of *X. derbentina* was 52.9% in May 2020; this fact attracted much attention. In previous years, the share of adults did not exceed 5% at the end of spring. Within its natural range, this species has an annual life cycle, when molluscs reach reproductive stage at the end of the season (end of summer–autumn), they spawn egg clutches for the next season, and most of them do not survive until next spring [Popov, Dragomoschenko, 1997]. In this case, very few adult specimens remain for the next season, as we observed clearly in 2017 and 2019. But in 2020, a significant proportion of adult specimens survived the winter. In the southeastern France, where *X. derbentina* is also an invasive species, it demonstrates a plasticity of life cycle [Kiss *et al.*, 2005]. This species can switch its life cycle from annual to biennial. At the moment, it is too early to say that the population of *X. derbentina* in Belgorod city has similar features. However, plasticity and shifts of the life cycle are quite typical for invasive species, in particular, xerophilous gastropods [Baker, Vogelzang, 1988]. This trait may also contribute to adaptation to conditions in a new habitat [Crowl, Covich, 1990; Masson, Brownscombe, 2016; Tibbets *et al.*, 2010].

The Caucasian land snail, *H. ravergiensis*, has a similar dynamics of the ratio of age classes for two years, when juveniles prevail at the beginning of the season, and adults at the end of the season. In 2020, a decrease in the population density of *H. ravergiensis* has been noted at the beginning of the season. We suppose that the main reason for this is a decrease in the average monthly temperature in May and June 2020. There were also changes in the proportion of juvenile and subadult snails in site 2: in May, the proportion of juveniles increased, and in June, the proportion of the subadult ones. The possible reason is the decrease in air temperature in May and June in 2020 that resulted in slower growth of juvenile snails. Nonetheless this feature has not been observed in most sites. We suppose that such a pattern during short observation time can be identified only in an area with a high population density as in the site 2.

Table 12. Estimation of Moran's index and spatial distribution in populations of xerophilous snails.

Таблица 12. Оценки индекса Морана и тип пространственного распределения в популяциях ксерофильных моллюсков.

Year	Month	Species	I_M*	z-score	p-value	Type of spatial distribution
2017	May	*B. cylindrica*	0.27	6.42	< 0.001	aggregated
		X. derbentina	0.11	2.67	0.010	aggregated
	June	*B. cylindrica*	0.11	2.65	0.010	aggregated
		X. derbentina	0.16	3.87	< 0.001	aggregated
	July	*B. cylindrica*	0.13	3.21	0.001	aggregated
		X. derbentina	0.15	3.67	< 0.001	aggregated
	Aug.	*B. cylindrica*	0.28	6.77	< 0.001	aggregated
		X. derbentina	-0.002	0.12	0.910	random
	Sept.	*B. cylindrica*	0.40	10.37	< 0.001	aggregated
		X. derbentina	0.04	1.05	0.290	random
2019	May	*B. cylindrica*	0.42	9.93	< 0.001	aggregated
		X. derbentina	-0.03	-0.51	0.607	random
	June	*B. cylindrica*	0.33	7.81	< 0.001	aggregated
		X. derbentina	-0.03	-0.81	0.418	random
	July	*B. cylindrica*	0.44	10.51	< 0.001	aggregated
		X. derbentina	0.01	0.42	0.676	random
	Aug.	*B. cylindrica*	0.40	9.59	< 0.001	aggregated
		X. derbentina	0.13	3.36	0.001	aggregated
	Sept.	*B. cylindrica*	0.44	10.59	< 0.001	aggregated
		X. derbentina	0.00	0.26	0.791	random
2020	May	*B. cylindrica*	0.34	8.34	< 0.001	aggregated
		X. derbentina	-0.02	-0.33	0.744	random
	June	*B. cylindrica*	0.27	6.56	< 0.001	aggregated
		X. derbentina	0.07	2.22	0.026	aggregated
	July	*B. cylindrica*	0.13	3.27	0.001	aggregated
		X. derbentina	0.02	0.77	0.443	random
	Aug.	*B. cylindrica*	0.32	7.82	< 0.001	aggregated
		X. derbentina	0.05	1.81	0.070	random
	Sept.	*B. cylindrica*	0.14	3.55	< 0.001	aggregated
		X. derbentina	0.05	1.50	0.134	random

Notes. *I_M - Moran's index

For population density of *H. ravergiensis*, a statistically significant correlation with the mean monthly temperature during the season of activity was found. The temperature was significantly lower in May and June 2020 than during previous years and the normal climate (Table 2). However, the population density did not change in 2020 compared to 2019 from July to the end of the season. For population density of *B. cylindrica* and *X. derbentina* such correlation is absent.

However, we argue that a decrease in the density of the population in the months with maximum temperatures is a possible reason, due to adaptive behavior of *B. cylindrica* to high temperatures and to high mortality of juveniles during this period (see above). In all species, there were significant differences in population density by years. We assume that the air temperature in winter is one of the limiting factors. In general, there have been changes in the temperature regime in the southern part of the Central Russian Upland over the past decades. The temperature during the cold months has increased, mainly from January through March. In the last decade, warming in July has also been added to this trend [Lebedeva *et al.*, 2016; 2019]. Over the three-year period of our observations, the winter of 2019-2020 was particularly noteworthy, when almost all winter months were frost-free. The vegetation season also began earlier than normal. We assume that these environmental changes promoted the increase of the population density of the *H. ravergiensis* and *B. cylindrica* in 2020. Most likely, this temperature anomaly observed in winter of 2019-2020 contributed to the survival of adults of *X. derbentina*, so a significant share of adult specimens was noted in the population in spring 2020.

Alien species of gastropods, settled currently in the southern part of the Central Russian Upland, are native to the Black Sea region. We suppose that trends in the climate warming of the Central Russian

Table 13. Estimation of Morisita index and spatial distribution in population of *Harmozica ravergiensis* on nine sites.

Таблица 13. Оценки индекса Морисита и тип пространственного распределения в популяции *Harmozica ravergiensis* на девяти пробных участках.

year	site	I_δ	p-value	Type of spatial distribution
2019	1	0.913	0.821	random
	2	>100	<0.001	aggregated
	3	0.649	0.996	random
	4	0.778	0.946	random
	5	0.650	0.999	random
	6	0.787	0.979	random
	7	1.073	0.295	random
	8	0.679	0.882	random
	9	1.031	0.400	random
2020	1	0.955	0.675	random
	2	1.115	0.011	aggregated
	3	0.488	0.999	random
	4	0.982	0.529	random
	5	0.731	0.988	random
	6	1.093	0.116	random
	7	1.097	0.264	random
	8	<0.001	0.984	random
	9	1.091	0.327	random

I_δ – Morisita index. Random spatial distribution I_δ=1; aggregated spatial distribution I_δ>1; even spatial distribution I_δ<1

Table 14. Bivariate spatial cross-correlation between the population density of *Brephulopsis cylindrica* and *Xeropicta derbentina* according to local Moran's-I (LISA), following Chen (2015).

Таблица 14. Двумерная пространственная кросс-корреляция между плотностью популяций *Brephulopsis cylindrica* и *Xeropicta derbentina*, согласно локальному I-критерию Морана (LISA), рассчитанному по Chen (2015).

Year	Month	LISA	*p*-value
2017	May	-0.577	< 0.001
	June	-0.189	0.193
	July	0.140	0.349
	Aug	-0.169	0.259
	Sept	-0.220	0.126
2019	May	-0.228	0.127
	June	-0.0421	0.764
	July	-0.143	0.316
	Aug	-0.369	0.017
	Sept	-0.143	0.311
2020	May	-0.082	0.488
	June	0.031	0.806
	July	-0.146	0.310
	Aug	-0.099	0.440
	Sept	0.295	0.048

Upland will contribute to the expansion of this territory by the warm-loving species. The dispersal of such gastropods across Europe has long been known [Peltanová *et al.*, 2012]. Climatic factors contribute to this process; in particular, the air temperature in January contributes much to the abundance of alien land snails in the cities of Central Europe in spring [Horsák *et al.*, 2016]. In addition, gastropods, inhabiting arid zone, are known to be most abundant in the areas with intermediate aridity levels [Moreno-Rueda, 2014]. The climatic conditions of the southern part of the Central Russian Upland will be favorable for the three studied species as well. There are other examples of the effect of climate change on the successful dispersal and expansion in new habitats by invasive molluscs, for example, for freshwater species *Sinanodonta woodiana* (Lea, 1834) [Spyra *et al.*, 2016] and land snail *Megalobulimus sanctipauli* (Ihering et Pilsbry, 1900*)* [Beltramino *et al.*, 2015].

Spatial population structure

Aggregated spatial distribution, observed in xerophilous species, is quite expected. A similar distribution has been reported for *B. cylindrica* population in the Dnepropetrovsk region [Kramarenko *et al.*, 2014]. There are several reasons for this type of spatial distribution. In populations of *B. cylindrica* and *Vallonia pulchella* (Müller, 1774), the heterogeneity in the composition of both soils and vegetation affect greatly the spatial structure of gastropod population [Kunakh *et al.*, 2018; Zhukov *et al.*, 2019]. The authors hypothesize that such site selectivity by snails may also reflect adaptation to arid climate. Many xerophilous gastropod species climb onto plants and form clusters [Riddle, 1983; Aubry *et al*., 2006]. This behavior is typical for the species of snails living in an arid climate with high level of insolation. Clustering behaviour has also been shown for rock-dwelling xerophylic land snails [Giokas, Mylonas, 2004]. The dependence of spatial organization on population density is well known, and species with a high population density often have a clustered structure [Montgomery, 2009].

In Belgorod city, the populations of *B. cylindrica* and *X. derbentina* are characterized by a correlation between the Moran's index, characterizing the type of spatial organization, and average population density (Spearman's test: rho = 0.741, $p < 0.001$, Fig.5). The change in spatial structure of *X. derbentina* population along with a simultaneous decrease in population density is especially interesting. In 2017, this species was characterized by a clustered distribution in most months, but the distribution was random in 2019 and 2020.

The spatial distribution of the *H.ravergiensis*

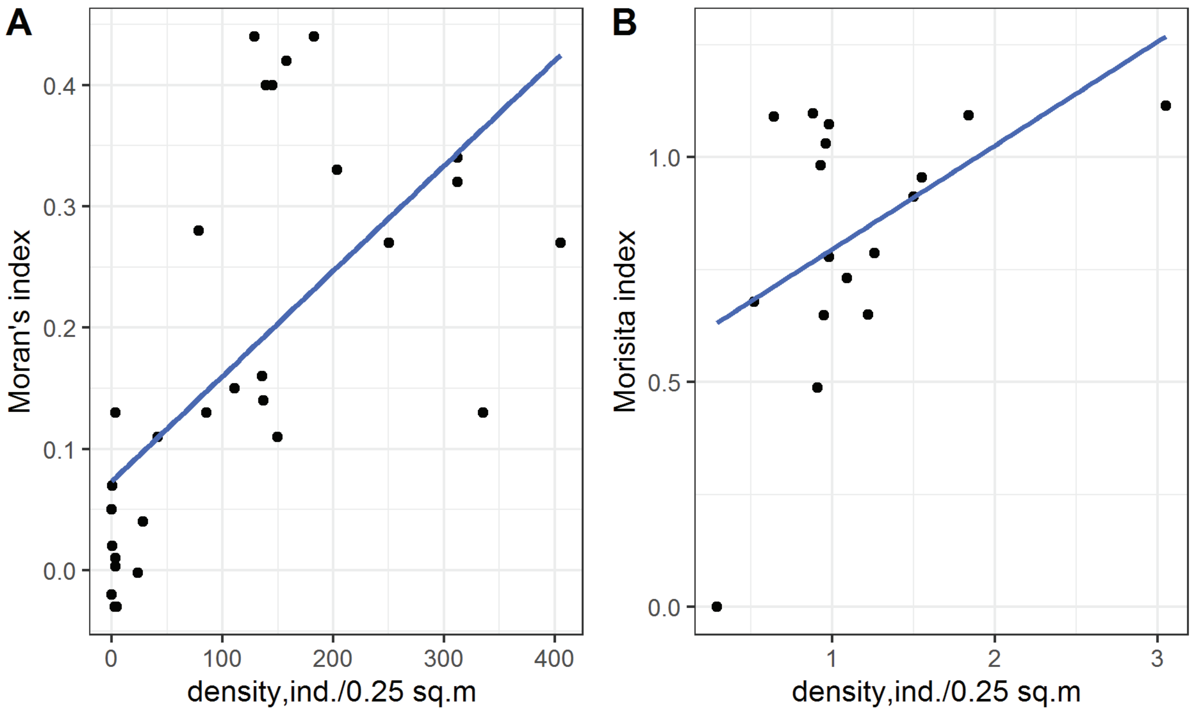

FIG. 5. Correlation between the spatial distribution index and population density. **A.** For *Brephulopsis cylindrica* and *Xeropicta derbentina* at 160 plots for three years. **B.** For *Harmozica ravergiensis* in nine sites×20 plots for two years.

РИС. 5. Корреляция между индексом пространственного распределения и плотностью популяции. **A.** Для *Brephulopsis cylindrica* и *Xeropicta derbentina* на 160 площадках за три года. **B.** Для *Harmozica ravergiensis* на девяти участках по 20 площадок за два года.

population in almost all sites was random except the site 2. We also performed a correlation analysis of the Morisita index and the average population density for *H.ravergiensis*, but did not obtain a statistically significant result (Spearman's test: rho = 0.457, p=0.056, Fig. 5). However, we want to highlight that the aggregated distribution was found at the site with the highest population density.

We also attempted to calculate the cross-correlation for *B. cylindrica* and *X. derbentina*. According to monthly calculations for three years, LISA had negative, but statistically insignificant values in most cases, except three of them (Table 14). This result ($p > 0.01$) may be explained by low abundance of *X. derbentina* in the study area. In 2019 and 2020, during the entire season, *X. derbentina* specimens were randomly distributed in this area (Table 12), represented by single specimens. In this regard, it was not possible to obtain a statistically significant result in calculating the cross-correlation coefficient. However, such inter-species interaction may be tracked by the change in the spatial organization of *X. derbentina* and a significant decrease in its abundance. Regard must be also paid to *H. ravergiensis* findings made until 2019, when this species was also found on the local site within the regular grid, and the spatial distribution of the population was random in 2017. However, already in 2019, no specimens of this species were found in this area, and the population density of the *H. ravergiensis* at the site no. 8 was assessed at a 200-m distance from the regular grid. We suppose that *H. ravergiensis*, as well as *X. derbentina*, was displaced from this site by *B. cylindrica,* characterized by an extremely high population density.

It is known that the inter-species interaction may play a decisive role in the development of biological invasions [Elton 1958; Hooper *et al.*, 2005]. Aboriginal species have often a negative impact on an invasive species [Holle *et al.*, 2003; Riley *et al.*, 2008]. The reverse situation is also possible. The example with *Bellamya chinensis* (Reeve, 1863) shows that native snail species were generally not found in areas where there was a high abundance of the invader [Solomon *et al.*, 2010]. High density of invasive snails may have an effect on the growth of juveniles of other species. Laboratory experiments on the effect of density on the growth of young freshwater snails demonstrated that an increase in abundance of the exotic apple snail *Pomacea insularum* (d'Orbigny, 1835) has the potential to reduce growth in the native apple snail *Pomacea paludosa* (Say, 1829) [Conner *et al.*, 2008]. Also the negative impact of the *P. canaliculata* on other snail species through different effects is shown both in the native and in the invasive ranges [Maldonado, Martín, 2019].

However, there are many examples of competitive interactions between two or more invasive species [Braks *et al.*, 2004; Hudina *et al.*, 2011; Johnson *et al.*, 2009; Platvoet *et al.*, 2009]. Apparently, at the first stages of expansion, a surge in the abundance of a certain alien species with a greater reproductive potential may negatively affect another alien species. It can be assumed that these species have different life strategies, when the spreading over a new habitat, which leads to such a pattern. In xerophilous snails, there are such examples [Yom-Tov, 1983]. Moreover, even the populations of the same non-indigenous species having a different population density may have a different influence of factors, such as natural enemies [Grason *et al.*, 2018]. We do not have enough data to explain the catastrophic decrease in the density of *X.derbentina* in our study. But we suppose that in this case we are observing the density effects of one species on another.

Summing up, we emphasize that our study will serve as the beginning of monitoring of the populations of alien terrestrial gastropods in the southern part of the Central Russian Upland. At this stage of research, we consider the *B. cylindrica* as the most successful invader, characterized by high population density and cluster spatial organization. We assume that this species suppresses locally other invaders, *X. derbentina* and *H. ravergiensis*. However, the dispersal of *H. ravergiensis* on the territory of the city and the increase of its population density allow this species to continue its expansion here. *X. derbentina* appears to be the least successful invader, although it exhibits certain plasticity of its life cycle and is potentially able adapt to the competing with *B. cylindrica*. In the natural range, both species coexist on the same territory, which also suggests such coexistence in the southern part of the Central Russian Upland. Warming observed in winter months favors the expansion. The population density of *X. derbentina* and *H. ravergiensis* also depends on the mean monthly temperature of the period of activity. That is why only abnormally cold summer may have a negative impact, but no such cases have been recorded in recent years. Therefore, we believe that the studied species will continue to expand their range northwards.

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