Acta Zoologica Academiae Scientiarum Hungaricae 68(3), pp. 247–260, 2022
DOI: 10.17109/AZH.68.3.247.2022

OCCURRENCE AND ABUNDANCE OF INVASIVE AND NATIVE *ARION* SLUGS IN THREE TYPES OF HABITATS IN URBAN AREA OF WROCŁAW (SW POLAND)

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Arion vulgaris and *Arion rufus* are two cryptic slug species whose ranges overlap in vast areas of Europe. In Poland, *A. rufus* is native; it reaches the eastern border of its range near Wrocław, while the invasive *A. vulgaris* was previously not recorded in this area. The study aimed to map the distribution of both species in the city of Wrocław and determine the size and abundance of their populations. Twenty-six sites were surveyed in 2019-2020. They represented three types of habitats: natural, semi-natural and anthropogenic. Because the investigated species are externally indistinguishable, their identification was based on the genital organs. Among 280 analysed specimens, 72% were identified as *A. vulgaris*, 23% as *A. rufus* and 5% were classified as hybrids. The hybrids and *A. vulgaris* were most abundant in semi-natural (83%) and anthropogenic habitats (95%), while *A. rufus* most often occurred in natural habitats (51%). *Arion vulgaris* occupied most of the sites (88.5%), and in 50%, it was collected alone. *Arion rufus* occurred in 46% of the sites (in 11.5% alone), and the hybrids were noted in 27%. In Wrocław *A. vulgaris* dominates in most sites, and its populations are much more abundant than those of *A. rufus* where the two species co-occur. This finding indicates that *A. vulgaris,* with its better adaptive skills and competitive abilities, may negatively impact the native species and, consequently, the latter's displacement. Although the recorded frequency of hybridisation was very low (5%), it may also have an effect on the local extinction of *A. rufus*. Interspecific hybridisation is assumed to foster invasions, and climate change may further exacerbate displacement; therefore, they should continue to be monitored.

Key words: Arionidae, Gastropoda, displacement, cryptic species, hybrids, SW Poland.

INTRODUCTION

Competition between species with overlapping ecological niches is generally driven by the limited availability of resources such as food, space or shelter (Pianka 1981, Connell 1983, Ferguson *et al.* 2013, Zwerschke *et al.* 2018). Competition for shared resources or interference between species increases with functional similarity and may lead to a displacement of the native species. It can cause a possible loss of related functional traits, which are considered

relevant to the response of organisms to the environment and/or their effects on the ecosystem (Elton 1958, Didham *et al.* 2005, Wardle *et al.* 2011, Dick *et al.* 2017). Competitive displacement (exclusion) often appears in the context of biological invasions and human-induced habitat modifications, both of which may threaten biodiversity (e.g. Mack *et al.* 2000). Within the rapidly expanding knowledge of species invasions, urban ecosystems seem to remain underexplored concerning the distribution, ecology and impact of non-native and invasive species (Francis & Chadwick 2015). Small habitat patches in cities are essential for various organisms, including those with poor dispersal abilities, that do not require large areas to maintain viable populations (McKinney 2008). Such places can act as local hotspots for both native and alien species.

Terrestrial gastropods are animals of low mobility. Some of them have managed to become established due to human introductions in European cities (e.g. Beckmann & Kobialka 2008, Říhová & Juřičková 2011, Dedov *et al.* 2015) or are even listed among invasive species (www.invasive.org). *Arion vulgaris* Moquin-Tandon, 1855, commonly known as the Spanish slug, is ranked among the hundred most invasive species in Europe (DAISIE 2009). *Arion vulgaris* and the native *A. rufus* (Linnaeus, 1758) are externally indistinguishable as adults and juveniles (Rowson *et al.* 2014b). Their identification is only possible based on the structure of the reproductive system, mating behaviour or molecular data (Quinteiro *et al.* 2005, Barr *et al.* 2009, Kałuski *et al.* 2011). Their taxonomy is problematic because data on the invasive species referred to *Arion lusitanicus* Mabille, 1868, which in fact, is an endemic species originating from Portugal. The invasive species spreading throughout Europe that commonly occur in an increasing number of countries is *A. vulgaris* (Zemanova *et al.* 2016, Zając *et al.* 2017). *Arion ater* (Linnaeus, 1758), occurring in Great Britain, Scandinavia, Iceland and northern Germany, is classified as a distinct species (Anderson 2005, Rowson *et al.* 2014*a, b*). Some researchers claim it is conspecific with *A. rufus*, but it is usually considered a separate subspecies. This question has been extensively reviewed by Reise *et al.* (2020), who, based on a thorough morphological investigation and COI mtDNA, recognise three subspecies i.e. *A. ater ater* (Linnaeus, 1758), *A. ater rufus* (Linnaeus, 1758) and *A. ater ruber* (Garsault, 1764). Here, we consistently use the name *Arion rufus* (Linnæus, 1758), probably corresponding to *A. ater ruber* in this area (Reise *et al.* 2020). Monitoring the distribution of *A. vulgaris* is especially problematic when *A. ater, A. rufus* and *A. vulgaris* co-occur in the same habitat. Moreover, it is difficult to distinguish *A. vulgaris* from other closely related, large congeners found in some parts of Europe, i.e. *A. magnus* Torres Mínguez, 1923, *A. flagellus* Collinge, 1893 and *A. lusitanicus*. The first reliable record of *A. vulgaris* in Poland dates from 1993 (environs of Rzeszów; podkarpackie voivodeship, SE Poland) (Kozłowski 2007). Though 1987 was mentioned as the probable date of its first appearance, there was no confirmed

identification (Stworzewicz & Kozłowski 2014). In 2001–2007 the slug spread rapidly in the south (voivodeships: małopolskie, śląskie, podkarpackie) and other regions of the country (voivodeships: łódzkie, mazowieckie, pomorskie, warmińsko-mazurskie and wielkopolskie) (Kozłowski 2008). Its occurrence in the western part of dolnośląskie voivodeship (= Lower Silesia) was also noted (Dreijers *et al.* 2013, Hutchinson & Reise 2015, Reise *et al.* 2020, Hutchinson *et al.* 2021), but there were no data from Wrocław, the largest city of this region, where *A. rufus* is native; its natural eastern border of distribution runs near Wrocław (Wiktor 2004, Kozłowski 2012).

This study aimed to characterise the populations of the two cryptic species co-occurring in three types of habitats (natural, semi-natural and anthropogenic) in the urban area of Wrocław. A detailed comparison of the distribution and abundance of the native *Arion rufus* and the invasive *Arion vulgaris* was intended to determine the actual occurrence of both species.

MATERIAL AND METHODS

The study was carried out in Wrocław in 2019-2020. The city is situated on the Odra River in the Sudetes foreland (SW Poland). The slugs were collected from 26 sampling sites in different parts of the city (Fig. 1). The habitat type (natural, semi-natural and anthropo-

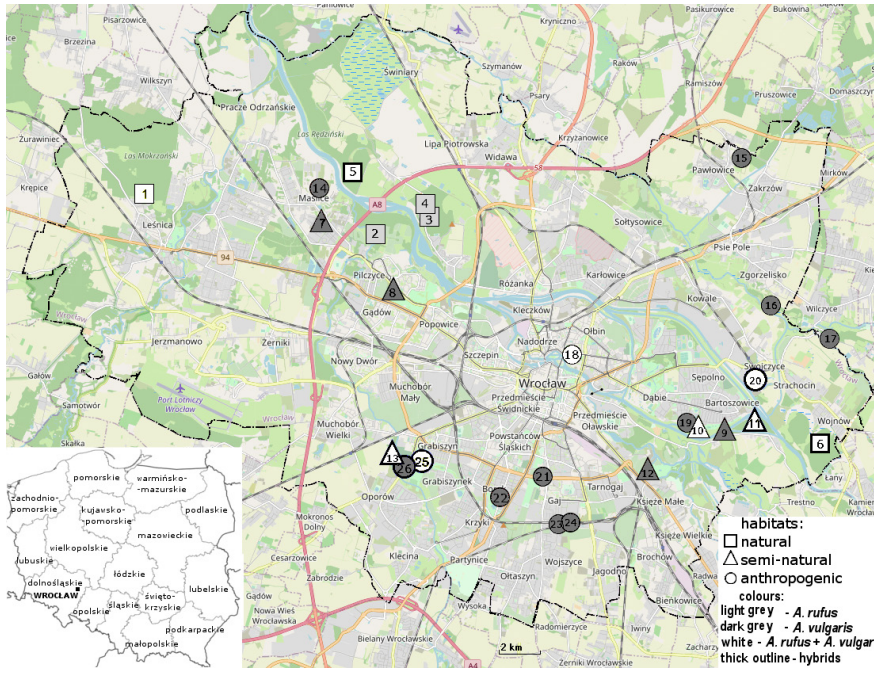

Fig. 1. Location of sampling sites in Wrocław (see Table 1) and map of administrative division of Poland. Symbols indicate the type of habitat. Colours indicate species and hybrids

genic) was recorded for each site. Forests (six sites) were classified as natural due to the insignificant level of their transformation (Fig. 2). Seven sites were regarded as semi-natural because of the relatively low level of anthropogenic transformation, the proximity of natural watercourses and the rich vegetation cover (Fig. 3). The remaining – anthropogenic sites showed signs of heavy human impact (Fig. 4). Table 1 shows detailed characteristics of the sites.

Table 1. Characteristics of sampling sites, collection data and identified *Arion* species. Abbreviations: HT = habitat type, nat = natural, sna = semi-natural, ant = anthropogenic.

No	Site	HT	Geographical coordinates	Collection date	Collector	Species
1.	forest Las Mokrzański	nat	51°09′38″N, 16°51′36″E	06.09.2020	E. Kuźnik-Kowalska	*A. vulgaris* – 1 *A. rufus* – 13
2.	forest Las Pilczycki	nat	51°08′59″N 16°57′36″E	05.2017	M. Proćków	*A. rufus* – 4
3.	forest Las Osobowicki	nat	51°09′16″N 16°59′00″E	01.08.2019	A. Wosinek	*A. rufus* – 3
4.	forest Las Osobowicki	nat	51°09′28″N 16°58′54″E	06.09.2020	E. Kuźnik-Kowalska	*A. rufus* – 13
5.	forest Las Rędziński	nat	51°09′59″N 16°57′01″E	06.09.2020	E. Kuźnik-Kowalska	*A. vulgaris* – 27 *A. rufus* – 9 hybrids – 2
6.	forest Las Strachociński	nat	51°05′34″N 17°09′10″E	08.09.2020	E. Kuźnik-Kowalska	*A. vulgaris* – 14 *A. rufus* – 4 hybrids – 1
7.	Maślice, Ostródzka street	sna	51°09′13″N 16°56′11″E	15.07.2020	E. Kuźnik-Kowalska	*A. vulgaris* – 10
8.	Park Zachodni	sna	51°08′06″N 16°58′04″E	15.07.2019	A. Wosinek	*A. vulgaris* – 1
9.	Biskupin, wał [flood bank]	sna	51°05′49″N 17°06′39″E	08.09.2020	E. Kuźnik-Kowalska	*A. vulgaris* – 13
10.	Park Biskupiński	sna	51°05′51″N 17°05′58″E	08.09.2020	E. Kuźnik-Kowalska	*A. vulgaris* – 15 *A. rufus* – 2
11.	island Wyspa Opatowicka	sna	51°05′58″N 17°07′26″E	08.09.2020	E. Kuźnik-Kowalska	*A. vulgaris* – 9 *A. rufus* – 9 hybrids – 1
12.	Park Wschodni	sna	51°05′09″N 17°04′40″E	14.07.2019	A. Wosinek	*A. vulgaris* – 9
13.	grove Lasek Oporowski	sna	51°05′25″N 16°58′02″E	21.08.2019	A. Wosinek	*A. vulgaris* – 8 *A. rufus* – 3 hybrids – 1
14.	Maślice, Północna street	ant	51°09′44″N 16°56′09″E	08.2019	E. Kuźnik-Kowalska	*A. vulgaris* – 2
15.	Pawłowice - Arboretum	ant	51°10′13″N 17°07′08″E	31.07.2019	E. Kuźnik-Kowalska	*A. vulgaris* – 6
16.	Zgorzelisko	ant	51°07′48″N 17°07′54″E	08.2019	J. Majk	*A. vulgaris* – 8
17.	Wilczyce	ant	51°07′18″N 17°09′21″E	08.2019	M. Mazurkiewicz-Kania	*A. vulgaris* – 5

Table 1 (continued)

No	Site	HT	Geographical coordinates	Collection date	Collector	Species
18.	Botanic Garden	ant	51°07′01″N 17°02′43″E	07.08.2019	M. Proćków	*A. vulgaris* – 22 *A. rufus* – 1
19.	Biskupin, Kożuchowska street	ant	51°05′54″N 17°05′41″E	09.2019	E. Kuźnik-Kowalska	*A. vulgaris* – 4
20.	Swojczyce	ant	51°06′37″N 17°07′27″E	15.07.2020	J. Mąkol	*A. vulgaris* – 14 *A. rufus* – 3 hybrids – 1
21.	Huby	ant	51°05′01″N 17°01′57″E	13.07.2019	A. Wosinek	*A. vulgaris* – 3
22.	Park Południowy	ant	51°04′41″N 17°00′51″E	13.07.2019	A. Wosinek	*A. vulgaris* – 6
23.	Wojszyce	ant	51°04′15″N 17°02′22″E	25.09.2019	A. Wosinek	*A. vulgaris* – 4
24.	Gaj	ant	51°04′16″N 17°02′40″E	03.07.2019	A. Wosinek	*A. vulgaris* – 2
25.	Park Grabiszyński	ant	51°05′17″N 16°58′48″E	07.08.2019	A. Wosinek	*A. vulgaris* – 6 *A. rufus* – 1 hybrids – 5
26.	Cemetery Grabiszyński	ant	51°05′11″N 16°58′21″E	07.08.2019	A. Wosinek	*A. vulgaris* – 12 hybrids – 3

Figs 2–4. Sampled habitat types: 2 = natural habitat in forest Las Pilczycki (locality no 2); 3 = semi-natural habitat with watercourse, the Dolna Oława in Park Wschodni (locality no 12); 4 = anthropogenic habitat in Maślice, Północna street (locality no 14)

The slugs were sampled by searching potential places of their occurrence, such as shrubs, shaded spots, fallen tree trunks, stone walls or moss-covered slabs. The presence of leaf litter and herbaceous plants, which are food for the slugs, was considered. Atmos-

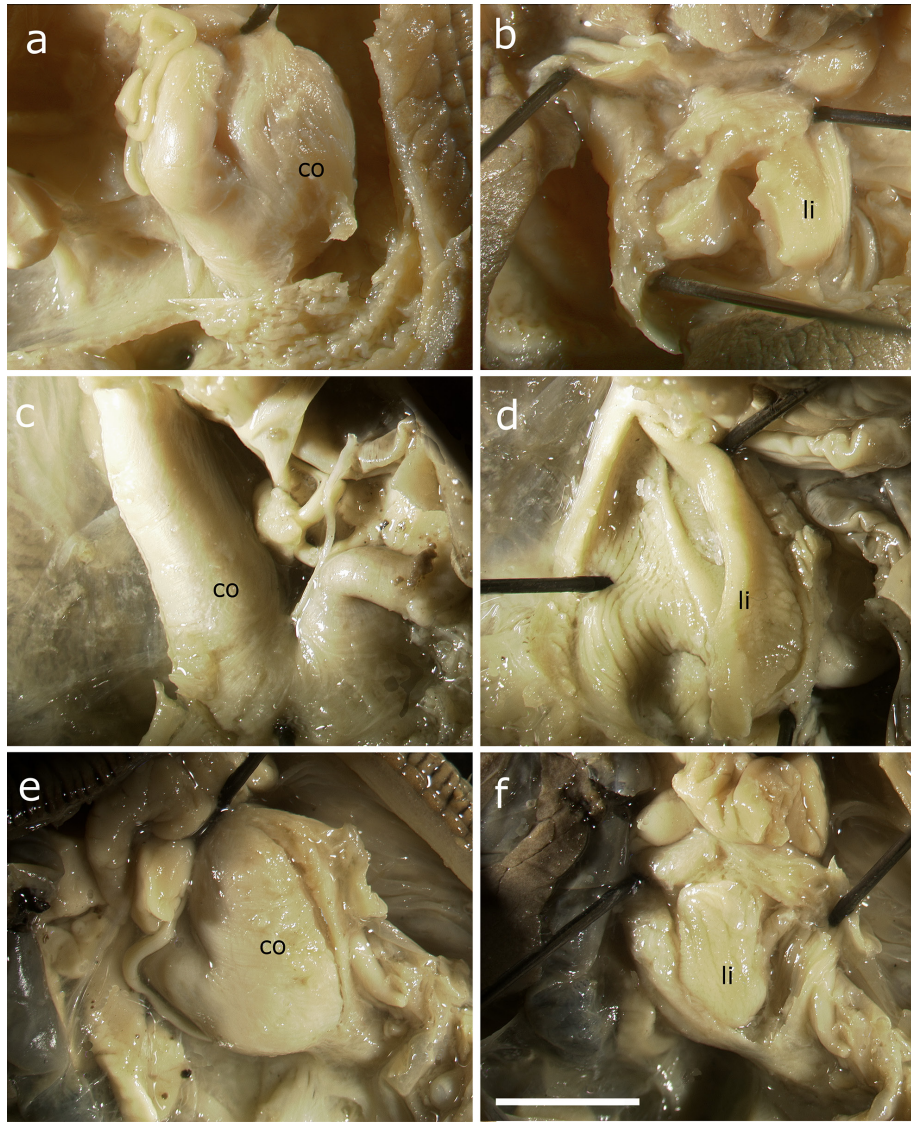

Fig. 5. Distal parts of the genitalia of *Arion rufus*: (a) upper atrium, (b) atrium opened to reveal the C-shaped ligula; *Arion vulgaris*: (c) long dilated part of oviduct, (d) distal oviduct opened to reveal the elongate, symmetric ligula; hybrid: (e) copulatory organ, (f) copulatory organ opened to reveal the ligula with an appearance of an oval plate. Abbreviations: co – copulatory organ, do – dilated oviduct, ep – epiphallus, li – ligula, ua – upper atrium. Scale bar 5 mm

pheric conditions were essential in order to make successful collections. The survey was carried out in the morning or after heavy showers. Only big specimens (ca. 10–15 cm long) were collected in order to minimise the risk of collecting juvenile slugs.

The slugs were drowned in boiled (deoxygenated) water at around 40 °C temperature. After approximately 8 h the specimens were rinsed with running water to remove the mucus. Afterwards, they were preserved in 70% alcohol. During dissection, the shape and size of atrium and oviduct were assessed, and then the oviduct was cut lengthwise to expose the ligula. A long dilated part of the oviduct with an elongate, symmetrical ligula was regarded as diagnostic for *A. vulgaris.* When a large and roughly C-shaped ligula was situated in a round upper atrium, the specimen was identified as *A. rufus* (Rowson *et al.* 2014*b*, Hatteland *et al.* 2015). In some cases the atrium and oviduct resembled those of *A. vulgaris*, but the oviduct was distended in its middle part, and the ligula was not symmetrical, but formed other shapes (Fig. 5). In general, all specimens which did not fit into the pure species were determined as potential hybrids, similar to other studies (Reise *et al.* 2020, Hutchinson *et al.* 2021). It was difficult to decide whether the ligula-bearing part should be called atrium or oviduct for the intermediate forms. Therefore, we used the term "copulatory organ". The total number of specimens studied was 280.

To compare the distributional data from our survey with those collected earlier, we used locality data of specimens deposited in the collections of the Museum of Natural History, Wrocław. They are as follows:

- Wrocław-Leśnica, 9.07.1974, leg. E. Pawłowska, 6 ex. dissected;
- Książ, 10-11.07.1974, leg. E. Pawłowska, 4 ex. dissected;
- Oława, no precise date, 5 ex. dissected;
- Wąwóz Myśliborski near Jawor, 29.07.1978, leg. B. Pokryszko, 1 ex. dissected;
- Lwówek Śląski, 4.10.1980, leg. B. Pokryszko, 2 ex. dissected;
- Janowice Wielkie, 26.05.1981, leg. B. Pokryszko, 1 ex. dissected;
- Trzebnica, 28.07.1988, leg. K. Bulman, M. Ciarka, 1 ex. dissected;
- Wilczyn near Trzebnica, 23.07.1988, leg. K. Bulman, M. Ciarka, 1 ex. dissected;
- Jaźwiny near Trzebnica, 5.07.1990, leg. K. Bulman, J. Pomorski, 1 ex. dissected;
- Krośnice, 29.06.1990, leg. K. Bulman, J. Pomorski, 1 ex. dissected.

RESULTS

The distributional data of *Arion* specimens, stored in the museum collection, are scarce in both Wrocław and its vicinity. In all ten localities sampled in the years 1974–1990 only *A. rufus* was then present (23 specimens). One of them, Leśnica is located within the boundaries of Wrocław, and the remaining ones 30–120 km in different directions from it. In contrast, our current results showed that both species, i.e. *A. vulgaris* and *A. rufus* as well as potential hybrids, occur in Wrocław. The greatest number of specimens were classified as *A. vulgaris* (72%), followed by *A. rufus* (23%) and hybrids (5%) (Fig. 6). In most sites, i.e. in 23 (88.5%), *A. vulgaris* dominated. *Arion rufus* occurred in 12 sites (46%), while the hybrids were recorded in seven sites (27%). *Arion rufus* co-occurred with *A. vulgaris* in three sites (11.5%), both species and the hybrids were recorded in six (23%), and in one (4%) *A. vulgaris* co-occurred with the hybrids. In three sites (11.5%), *A. rufus* occurred alone, whereas *A. vulgaris*

alone was found in 13 sites (50%). It should be noted that some sites were very lightly sampled (Fig. 6). Therefore, these data are bound to underestimate the proportion of sites in which the species coexist.

Geographically the hybrids co-occurred with one or both species mainly in the south-western and south-eastern parts of Wrocław, in all types of habitats (Fig. 1). Both species, without hybrids, were found at three sites of different habitats and distribution. The forests, i.e. Las Osobowicki (16 specimens) and Las Pilczycki (4 specimens), located in the north-western part of the city, were the only places where only *A. rufus* was recorded. These forests are the most natural habitats in the studied area. In the remaining sites (50%), both semi-natural and anthropogenic (e.g. gardens, cemeteries, parks), only *A. vulgaris* was present.

DISCUSSION

Competition is one of the essential forces of natural selection and a driver of dispersal, the process that allows species for permanent or temporary coexistence. Competition is particularly strong between closely related species with similar requirements and shares common niche spaces. Consequently, this either leads to the extinction of the weaker competitor or to a genotypic or phenotypic shift towards a different niche (Krebs 2009). In a vast part of Europe,

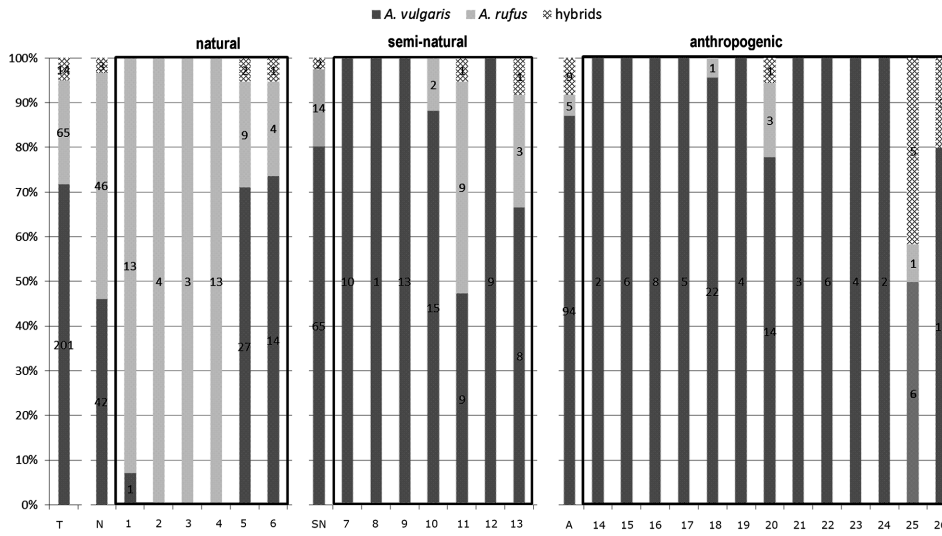

Fig. 6. Number and proportion of *A. vulgaris*, *A. rufus* and hybrids found in sites studied in Wrocław. Sites are divided according to habitat type: natural (N), semi-natural (SN) and anthropogenic (A), total (T). Numbers on horizontal axis refer to sampling sites detailed in Table 1

the ranges of *A. rufus* and *A. vulgaris* currently overlap (Welter-Schultes 2012). Our results show that the species are common in Wrocław, but they occur in unequal proportions. *Arion vulgaris* dominates in most places, although it was not recorded there several years ago (Wiktor 2004, Kozłowski 2012). Both species are expanding their ranges to the east (Kozłowski 2012), but *A. vulgaris* has spread faster, and in Wrocław, it dominates over the native *A. rufus*, which is definitely less frequent and forms much smaller populations. This is also the case in other nearby urban areas (Hutchinson & Reise 2015, Ludwig *et al.* 2015). *Arion rufus* was earlier recorded in only one locality, in the Wojszyce settlement, located in the southern part of Wrocław (Kosińska 1979). Now the invasive *A. vulgaris* was found there (locality no 23) and in the surrounding area (Fig. 1). Although limited, the museum data show that before 1990 only *A. rufus* occurred in the vicinity of Wrocław and was probably more common in the city itself than the literature indicates (Kosińska 1979). Unlike other studies, our results do not provide direct evidence that the invasive *A. vulgaris* contributed to local extinctions of the native *A. rufus* (Winter 1989, Rüetschi *et al.* 2012, Dreijers *et al.* 2013, Zemanova *et al.* 2017), or *A. ater* in northern Europe (Hagnell *et al.* 2004, Roth *et al.* 2012, Hatteland *et al.* 2015). However, we showed that its populations are larger and more abundant, which allows *A. vulgaris* to outcompete the native *A. rufus* by greater survivorship and better ability to use new resources (Ryser *et al.* 2011, Kappes *et al.* 2012, Blattmann *et al.* 2013).

Introgression and hybridisation are the factors that influence invasiveness and expansion patterns (Rhymer & Simberloff 1996). Despite the mechanical and behavioural reproductive isolating mechanisms, *A. vulgaris* and *A. rufus* can crossbreed both in the laboratory (Roth *et al.* 2012, Dreijers *et al.* 2013) and in the wild (Allgaier 2015, Zemanova *et al.* 2017). Some studies suggest that, in the field, successful interspecific mating in terms of spermatophore transfer probably occurs only at very low frequencies (Allgaier 2015). In captivity also, merely 16% of all copulations compared to intraspecific pairs were successful (Dreijers *et al.* 2013). However, this would not prevent genetic admixture, suggesting recurrent hybridisation beyond the first generation (Zemanova *et al.* 2017). Very detailed genetic studies using microsatellites also confirmed many cases of hybridisation (Hutchinson *et al.* 2021), although only ca. 4% of the population had anatomies identified as hybrids (Reise *et al.* 2020). Our results based on anatomical identification revealed a small proportion of hybrids (5%), which partly may be due to poor sampling on a few sites; however, genetic data indicate that hybridisation is not rare (Hatteland *et al.* 2015, Zemanova *et al.* 2017). It is suspected to be one of the mechanisms underlying the regional decline of the native species (Zemanova *et al.* 2017).

Some studies show differences in habitat preferences between *A. vulgaris* and *A. rufus*, pointing out that *A. rufus* is associated with woodlands, while *A. vulgaris* mainly occurs in anthropogenic areas (Riedel & Wiktor 1974,

Wiktor 2004, Allgaier 2015, Zając *et al.* 2017). Similar relationships were observed in Wrocław, i.e. *A. rufus* is primarily confined to natural habitats, whereas *A. vulgaris* is present in urbanised, sometimes much transformed places. Likewise, *A. ater* and *A. vulgaris* and their hybrids were observed to differ in their habitat preferences. *Arion ater*, native in Norway, occupies natural or semi-natural habitats (e.g. heathlands, forests), the invasive *A. vulgaris* prefers strongly transformed habitats, and the hybrids occur in gardens and parks (Hatteland *et al.* 2015). *Arion vulgaris* is more prone to explore new areas and is better at handling anthropogenic transformation (Zemanova *et al.* 2017). However, our study shows that it easily penetrates semi-natural and natural habitats, where it dominates over the coexisting native *A. rufus*. In the mid-19th century, this slug was recorded in gardens and forests in our area (Silesia) (Scholtz 1843) and then generally in Poland; it was thought to avoid developed environments (Riedel & Wiktor 1974). At present, it also inhabits anthropogenic environments such as ditches, roadsides, cemeteries, parks and rubbish dumps, as well as agrocenoses (Kozłowski 2012). *Arion vulgaris* first appeared in SE Poland in the 1990s, and since then, it has spread rapidly in other regions of the country (Kozłowski 2008). However, it is not known when exactly it reached Wrocław. It might be brought along with human activities; thus, it first penetrated anthropogenic environments of the city (allotments, gardens, parks, etc.), and over time it could successively occupy semi-natural and natural habitats. This may have happened in the last two or three decades. It can be assumed that in anthropogenic environments *A. vulgaris*, as a species that can tolerate dryer habitats, can displace *A. rufus*, which more often inhabits places in the vicinity of watercourses and water bodies, riparian forests. Populations of *A. rufus* are numerous and stable in such habitats, and if *A. vulgaris* reaches those areas, it becomes a co-occurring species, and interspecific hybridisation could also take place. Climate change promotes the risk of biological invasions. Periods of multi-day heat and drought recently observed in our region during summer, and early autumn may significantly affect the survival of both species. However, the tolerance of *A. vulgaris* to survive in low temperatures and droughts (Slotsbo *et al.* 2011*a, b*) ultimately gives it an advantage over *A. rufus*. Considering this and the great reproductive potential, non-selective diet and the ability to self-fertilise (Hagnell *et al.* 2006, Kozłowski & Kozłowski 2011), the invasive species poses a threat to the local biodiversity. Despite a possible shrinkage of the suitable areas for the genus *Arion* in the future, new ones will also appear, such as Iceland, northern Scandinavia or equatorial regions (Zemanova *et al.* 2018).

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Acknowledgements – We are thankful to Marta Mazurkiewicz-Kania, Joanna Mąkol and Jakub Majk for providing some samples and Beata M. Pokryszko for improving the

English. We are immensely grateful to John Hutchinson and Barna Páll-Gergely for their helpful comments and valuable remarks on the manuscript.

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Revised version submitted April 11, 2022; accepted April 30, 2022; published August 12, 2022