

## ARION VULGARIS MOQUIN-TANDON, 1855 – THE AETIOLOGY OF AN INVASIVE SPECIES

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**ABSTRACT:** *Arion vulgaris* Moquin-Tandon, 1855 is ranked among the hundred most invasive species in Europe. Its native range is not known for certain. For many years, it was believed that the slug came from south-western Europe and began its spread over 40 years ago in the Iberian Peninsula, but recent molecular data suggest that it is native to Central Europe. Here we present a review of its biology, nomenclature, distribution, characteristics, control methods and status. We discuss potential reasons for the great success of *A. vulgaris*, considering various hypotheses which may explain its invasiveness.

**KEY WORDS:** *Arion vulgaris*, invasive species, review, slugs

### INTRODUCTION

The current homogenisation of the Earth's biota, which is caused by the spread of alien (i.e. non-indigenous) and invasive (i.e. non-indigenous and harmful) species, is a major threat to global biodiversity. Such species have enormous impact on biological communities: they not only cause the loss of biodiversity but also generate high economic costs (DAVIES 1987, FRANK 1998, WALTHER et al. 2009, KOZŁOWSKI & KOZŁOWSKI 2011). According to various authors, invasive species share the following characteristics: high fertility, rapid development, great ecological tolerance, drought resistance (in case of terrestrial species, crucial given climate change), few natural enemies, good dispersal abilities, greater survivorship at higher temperatures, behavioural plasticity, and greater phenotypic plasticity compared to native species (KOLAR & LODGE 2001, SIMBERLOFF 2001, KNOP & REUSSER 2012). These traits facilitate colonisation of new territories, with their novel thermal conditions and food resources.

Commonly known as the Spanish slug, *Arion vulgaris* Moquin-Tandon, 1855 which for many years has been called *A. lusitanicus*, belongs to the Arionidae and is ranked among the hundred most invasive

species in Europe (RABITSCH 2006). *A. vulgaris* has, probably unintentionally, been introduced into new habitats via plant matter, packaging, and waste materials (KOZŁOWSKI 2007). It is a major defoliator of plants and causes severe damage in orchards and gardens as well as serious crop losses; for example, it has been observed to reduce strawberry yields in Sweden by half (GREN et al. 2009). The slug also transmits plant pathogens (WEIDEMA 2006, HATTELAND 2010, PELTANOVÁ et al. 2011, KOZŁOWSKI 2012, SLOTSBO 2012) and is an intermediate host of a nematode parasite of dogs and foxes – *Angiostrongylus vasorum* (Baillet, 1866) (FERDUSHY et al. 2010). In Sweden, it is suspected that slug-contaminated silage causes health problems in animals during wet summers. Densities of over 50 slugs per square metre have been observed in wildflower strips and meadows. Such high numbers of slugs might contaminate grass silage and cause a potential threat to the safety and quality of animal feed (GISMERVIK et al. 2015). Furthermore, because of its large size and high population densities, *A. vulgaris* can outcompete native slug species; it may also reduce the biodiversity of wild plants (FRANK 2003).



## NOMENCLATURE AND DISTRIBUTION

*A. vulgaris* was first described from France in 1855 among varieties of *Arion rufus* (MOQUIN-TANDON 1855). In 1907, Taylor claimed that it was the same species as *A. ater* var. *rufa* or *A. subfuscus* Draparnaud, 1805 (TAYLOR 1907). Later, VAN REGTEREN ALTENA (1956) stated that it was actually *Arion lusitanicus* Mabille, 1868. However, CASTILLEJO (1997) discovered that it was a different species that was concerned. *A. lusitanicus*, which was described by MABILLE (1868), is common in central Portugal, and differs from the Spanish slugs found throughout Europe in both external appearance and genital morphology. Molecular analyses confirmed that *A. vulgaris* and *A. lusitanicus* were actually distinct species (QUINTEIRO et al. 2005). These findings induced researchers to use the name *A. vulgaris* which was proposed by FALKNER et al. (2002). Consequently, in the older literature the name *A. lusitanicus* used for the large invasive *Arion* occurring in Europe most probably refers to *A. vulgaris*.

The native range of *A. vulgaris* is not known for certain. For many years, it was believed that the slug came from south-western Europe (ROTH et al. 2012) and began its spread over 40 years ago in the Iberian Peninsula. Its original distribution included Spain, Portugal and the Azores (SIMROTH 1891, QUICK 1952, 1960, VAN REGTEREN ALTENA 1971, CHEVALLIER 1972). It appears that *A. vulgaris* has ex-

panded its range in many European countries over the last five decades. At present, it occurs in France (1855), Great Britain (1952), Germany (1970), Slovenia (1970), Italy (1971), Switzerland (1971), Austria (1972), Sweden (1975), Bulgaria (1983), Austria (1984), Norway (1988), Belgium (1989), The Netherlands (1989), Finland (1990), Denmark (1991), Poland (1993), Iceland (2003–2004), Greenland, Latvia, and Lithuania and has more recently appeared on the Faroe Islands (QUICK 1952, 1960, ELLIS 1965, SCHMID 1970, VAN REGTEREN ALTENA 1971, RIEDEL & WIKTOR 1974, DAVIES 1987, DE WINTER 1989, VON PROSCHWITZ 1992, 1994, VON PROSCHWITZ & WINGE 1994, WIKTOR 1996, WEIDEMA 2006, KOZŁOWSKI 2007, SLOTSBO 2012). It has recently arrived in Romania (PĂPUREANU et al. 2014). However, some recent findings contradict the idea of the Iberian origin. PFENNINGER et al. (2014) suggested that it was highly probable that the species was actually native to central Europe: phylogeographic analyses using mitochondrial (COI) and nuclear (ZF) markers combined with species distribution modelling found that no haplotypes from Spain or western France co-occurred with those from central Europe. This discovery aside, *A. vulgaris* clearly exhibits invasive features in the countries where it has most recently appeared.

## DISTINGUISHING BETWEEN SPECIES

Monitoring the spread of *A. vulgaris* is challenging because the species is difficult to distinguish from the other closely related, large arionids (*A. ater* Linnaeus, 1758; *A. rufus* Linnaeus, 1758; *A. magnus* Torres Minguez, 1923; *A. lusitanicus* Mabille, 1868; *A. flagellus* Collinge, 1893) which occur in Europe. When they co-occur in the same habitat, *A. ater*, *A. rufus*, and *A. vulgaris* can only be identified by virtue of their genital morphology, mating behaviour or by molecular methods because the three species are very similar in external appearance (QUINTEIRO et al. 2005, BARR et al. 2009, KAŁUSKI et al. 2011, SLOTSBO 2012). *A. vulgaris* has the following species-specific features: atri-

um small, almost symmetrical and uni-partite, bursa copulatrix oval, fallopian tube with a short, thin posterior end and a thick, rapidly expanding anterior part, long oviduct with a large ligula inside (WIKTOR 2004, WELTHER-SCHULTES 2012). Mating of *A. vulgaris* takes from 4 to 5.5 hours from the moment of finding a partner to separation after mating, while in *A. rufus* the process takes 3 hours (KÜNKEL 1908, FRÖMMING 1954, KOZŁOWSKI 2007). To complicate matters further, *A. ater* and *A. rufus* can hybridise, and there is some evidence that they hybridise with *A. vulgaris* as well (EVANS 1986, ROTH et al. 2012, DREIJERS et al. 2013).

## CONTROL METHODS

One method for controlling pests slugs and snails is the use of molluscicides, such as metal salts (iron [III] phosphate), metaldehyde, and acetylcholinesterase inhibitors (methiocarb) (CLEARWATER et al. 2008). Traps containing molluscicide pellets are highly successful in attracting slugs because they present

favourable microclimatic conditions and bait with an olfactory appeal. Additionally, the traps ensure that the molluscicide is not exposed to the elements and prevent it from being consumed or dragged away by other animals (GRIMM & SCHAUMBERGER 2002). However, the use of molluscicides to control the



Spanish slug can have negative effects (WEIDEMA 2006). Chemical molluscicides are toxic to several non-target vertebrate and invertebrate species and can not be used on organic farms (FRANK et al. 2002). Some of the molluscicides that effectively target *A. vulgaris* contain iron phosphate and EDTA or EDDS, and may therefore have adverse effects on the activity or growth of earthworms, or may even be toxic to

them. Consumption of molluscicides can be dangerous to domestic animals and cattle (EDWARDS et al. 2009). Moreover, molluscicides can bioaccumulate in slug predators and are likely to affect soil-inhabiting invertebrates such as beetles, millipedes, and woodlice, but further studies on the subject are needed (EDWARDS et al. 2009).

## BIOLOGY OF *A. VULGARIS*

*A. vulgaris* has an annual life cycle and is semelparous; although it mainly reproduces sexually, it can also self-fertilise (HAGNELL et al. 2006, KOZŁOWSKI 2007, SLOTSBO 2012). Adult slugs can reach 14–15 cm in length but are usually smaller, around 11 cm, and range in colour from orange to chocolate brown to black, with black, brown, or orange foot fringe (KOZŁOWSKI 2007, ROTH et al. 2012, SLOTSBO 2012). As a result, the colouration cannot be used to distinguish *A. vulgaris* from *A. rufus* (WIKTOR 2004). Mating occurs when the slugs are in the male phase, from July to October; it is very complex and can last as long as 4–5 hours (KOZŁOWSKI 2007, ROTH et al. 2012, DREIJERS et al. 2013). The slugs begin to lay eggs when they reach the non-mating female phase (two to four weeks after copulation); the egg-laying period starts in August and can last until December if temperatures remain above 5°C. The exact time varies between geographical regions and years (KOZŁOWSKI & KOZŁOWSKI 2000, GRIMM 2001). The Spanish slug can lay a total of 400–500 eggs in batches with the mean size of 67.3 eggs (KOZŁOWSKI 2007, SLOTSBO 2012). KOZŁOWSKI & KOZŁOWSKI (2000) found that most egg-laying slugs were aged 6–9 months; however, it was unclear whether age, season, or body mass affected the egg-laying ability. Although most slugs (75%) die having reproduced, some winter over and, in the laboratory, may live for as long as three years, provided they do not reproduce (SLOTSBO 2012). Indeed, they can delay their reproduction until the following mating season. This ability allows the species to tolerate harsh climatic conditions and perhaps better handle different situations, such as the arrival in new areas where mating may be restricted by small population densities (SLOTSBO et al. 2013). Hatching starts in September, and 54–86% of eggs hatch before winter (KOZŁOWSKI 2007). Later-laid eggs winter over and hatch in the spring (KOZŁOWSKI 2007). The hatching success is the highest at 10–15°C (SLOTSBO 2012). The thermal tolerance may therefore vary geographically among populations (SLOTSBO et al. 2013). The eggs are rather cold-tolerant: the hatching success remains higher than 79% for eggs exposed to the temperature of –1.3°C. However, at temperatures lower than –4°C all the eggs freeze. The eggs are also

drought-resistant: the hatching success is unaffected even when up to 63–70% of the initial water content is lost (SLOTSBO 2012). As in many other invertebrates, the growth is influenced by temperature; it is fastest at 20°C (KOZŁOWSKI 2007, SLOTSBO 2012). At 25°C, the eggs fail to develop and hatch, suggesting it is the upper temperature limit for the species (KOZŁOWSKI 2000). The slugs can stand lower temperatures (although they almost completely stop growing at 2–5°C) without any significant impact on their survivorship. Most juveniles and some adults can survive being frozen at –1.3°C. Small juveniles can stay super-cooled at –3°C for 20 days. The ability of juvenile *A. vulgaris* to remain active at –3°C allows them to move to deeper, frost-free microhabitats even in sub-zero temperatures (SLOTSBO 2012). Juvenile and adult slugs must also endure desiccation pressures. The survivorship of juvenile *A. vulgaris* was unaffected as long as their water loss did not exceed 56% (SLOTSBO 2012). *A. vulgaris* displays a remarkable degree of plasticity: even after growing very slowly for a year, the slugs immediately increase their growth rate when exposed to higher temperatures. In the spring, this means that overwintering juveniles can start growing as soon as temperatures rise, provided that food is abundant. Further evidence of this plasticity is provided by an experiment carried out by SLOTSBO et al. (2013). Slugs kept at 2°C and 5°C were then moved to 15°C, and their growth rate rapidly increased. The slugs' growth rate is correlated with temperature, which is beneficial for the animals because of food limitations during the year when their metabolic requirements are low (SLOTSBO et al. 2013).

Among the environmental factors studied to date, photoperiod has the greatest effect on *A. vulgaris*. The species' activity patterns have been found to be similar both in the field, under fluctuating temperatures, and in the laboratory, under constant temperatures. For many animal species, including slugs (e.g. *Limax maximus* Linnaeus, 1758), photoperiod is a seasonal cue that controls the annual reproductive cycle. It could very well control maturity in *A. vulgaris* (GRIMM & SCHAUMBERGER 2002, SLOTSBO et al. 2013). *A. vulgaris* was most active at 5:30, 1.5 h after sunrise, and



at 20:30, 1 h after sunset; it was least active between 13:00 and 14:00. Over 24 hours, the slugs spent 68% of their time resting, mainly under artificial shelter traps, 27% of their time in locomotion, and 4% of their time feeding (GRIMM & SCHAUMBERGER 2002). A similar pattern of activity has been observed in *A. distinctus* Mabille, 1868: it is the most active at 7:30, 0.5 h after sunrise and from 19.30 to 2.00 (HOMMAY et al. 1998).

*A. vulgaris* is polyphagous and feeds on a range of crop species as well as waste products, animal carrion, and faeces (KOZŁOWSKI & KOZŁOWSKA 2004, TOMASGÅRD 2005, KOZŁOWSKI 2007). A test involving 78 plant species showed that *A. vulgaris* preferred plants of the families Brassicaceae, Papaveraceae, Apiaceae, Boraginaceae, and Asteraceae (BRINER & FRANK 1998). In the field, it was observed to forage on diverse genera, such as *Papaver*, *Solanum*, and *Lupinus* (AGUIAR & WINK 2005). All these plants contain potentially toxic compounds. These findings indicate that the presence of physical deterrents has a greater influence on food selection in *A. vulgaris* than do chemical defences. AGUIAR & WINK (2005) showed that *A. vulgaris* could tolerate very high levels of neurotoxic alkaloids because of the effective alkaloid detoxification in the microsomes in their digestive glands. Thanks to their inducible detoxification system, the slugs can feed on toxic plants when less toxic food is not available (AGUIAR & WINK 2005). Furthermore, JENSEN et al. (2013) found that due to their behavioural and physiological mechanisms *A. vulgaris* could regulate their protein and carbohydrate intake and utilisation in a way that made it possible for them to achieve an optimal balance that maximises growth (JENSEN et al. 2013). This trait should allow the slugs to more easily respond to changes in food availability.

*A. vulgaris* is not a prey item favoured by most predators (VON PROSCHWITZ & WINGE 1994, VON PROSCHWITZ 2008). It is apparently less palatable because it is harder to eat and produces more mucus than other, native slugs, such as *A. ater*, a species endemic to central and western Europe. The natural enemies of *A. vulgaris* are hedgehogs, amphibians, reptiles, and certain bird species. Larger ground beetles feed on eggs and young slugs (HATTELAND 2010). Cannibalism among Spanish slugs has also been observed but probably only becomes appreci-

able at high densities; furthermore, only dying slugs are attacked (WEIDEMA 2006). One of the biological control methods currently used to fight *A. vulgaris*, as well as other slugs (e.g. *A. rufus*, *Deroceras reticulatum*) is the application of Nemaslug, which contains a parasitic nematode (*Phasmarhabditis hermaphrodita*) that hosts the bacterium *Moraxela osloensis*. The result is reduced feeding and increased mortality. The method is most effective when individual doses (15 and 30 individuals/cm<sup>2</sup>) are applied to juveniles (TAN & GREWAL 2001, RAE et al. 2009). A very promising biological control agent may be *Carabus nemoralis*, a beetle capable of reducing densities of *A. vulgaris* in the wild (PIANEZZOLA et al. 2013).

Like most slugs, *A. vulgaris* is only found in moist habitats. Within its native range, the Spanish slug lives in grasslands and broadleaf deciduous woodlands (RABITSCH 2006). In its invaded range it occurs in gardens and parks (in areas with cultivated plants), cemeteries, agricultural and landscaped areas, and other anthropogenic habitats (KOZŁOWSKI et al. 2008). The species shows a preference for crops grown on loamy soil. Trade and human migration are thought to have aided introduction of new species to many parts of the world (MANCHESTER & BULLOCK 2000). *A. vulgaris* is a typical synanthropic species: its occurrence is associated with human activity (WEIDEMA 2006, KOZŁOWSKI 2007). Moreover, colonisation by *A. vulgaris* often results from passive transport, as the slug travels with cultivated plants (DREIJERS et al. 2013).

From the earliest days of invasion, it was postulated that genetic variation and evolution might play an important role in the success of invasive species. A growing number of studies show that putatively adaptive traits have evolved in introduced populations (e.g. HENDRY & QUINN 1997, HUEY et al. 2000, KOSKINEN et al. 2002, BLAIR & WOLFE 2004, ROGERS & SIEMANN 2004), sometimes quite rapidly (e.g. THOMPSON 1998, REZNICK & GHALAMBOR 2001). Certain specific life history traits and behaviours, as well as the degree of phenotypic plasticity, could account for the establishment of the numerous populations found in so many European countries. However, a more complete explanation for its invasiveness is lacking. Below, we discuss hypotheses that could shed some light on the Spanish slug's success.

## POTENTIAL REASONS FOR THE GREAT SUCCESS OF *ARION VULGARIS*

### TRAITS ENHANCING COMPETITIVENESS

One of the hypotheses which explain invasiveness postulates that invasive species have a suite of traits that enhance their performance relative to that

of native species over a broad range of conditions (JANION et al. 2010). This hypothesis was repeatedly tested. For example, JANION et al. (2010) found that, on Marion Island, invasive springtail species had much faster egg development rates, as well as a



lower susceptibility to hatching failure at higher temperatures, than did indigenous species. It is thought that *A. vulgaris* outcompetes the autochthonous *A. ater* and *A. rufus* (VON PROSCHWITZ 1997, KAPPES & KOBIALKA 2009, ROTH et al. 2012, DREIJERS et al. 2013, HATTELAND et al. 2013). In zones where the species co-occur, the native slugs have shrinking populations and are rarely seen in the same areas as *A. vulgaris* (GRIMM & PAILL 2001). *A. vulgaris* may derive part of its competitive advantage from its unique behaviour. KAPPES et al. (2012) found that the species was more active and less sensitive to adverse stimuli than were native slugs. It could be the cause of the appearance of this species in new habitats. As opposed to the native snails or slugs, *A. vulgaris* positively responds to baits containing acidic Renner solution, mustard oil, and garlic extract (KAPPES et al. 2012).

Dispersal could be enhanced by the Spanish slug's mobility. KNOP et al. (2013) compared the mobility of *A. vulgaris* with that of *A. rufus*, a native species, in an area where the two were sympatric. The main hypothesis was that *A. vulgaris* – the invader – had a higher moving rate (kept moving once in motion) and leaving rate (probability of being found in a new location) than the native slug. The study was carried out in three different habitats: a stubble field, an area sown with wild flowers, and a pasture. In all three habitats, *A. vulgaris* had higher moving and leaving rates. These results suggest that the Spanish slug's higher level of motor activity could explain its invasiveness (KNOP et al. 2013). It is notable that when slugs compete for the best shelters, *A. vulgaris* wins out over very aggressive species such as *A. subfuscus* (Draparnaud, 1805) and *Limax maximus* (GRIMM & PAILL 2001). When population densities are high, *A. vulgaris* will also inhabit less favourable areas, which indicates its flexibility and shows that it is a habitat generalist rather than a habitat specialist (GRIMM & PAILL 2001).

## PHENOTYPIC PLASTICITY

Short-term phenotypic plasticity is a major tool used by organisms to respond to environmental change, and when a population's circumstances shift, it helps determine whether the population will persist or disappear and thus whether or not it has potential for invasion (CHOWN et al. 2007). BAKER (1965) was the first to hypothesise that invasive species had greater phenotypic plasticity than native ones and to notice that genetic variation could be advantageous even to those species which had a high plasticity (DLUGOSCH & PARKER 2008). In a meta-analysis DAVIDSON et al. (2011) showed that invasive species had a significantly greater degree of phenotypic plasticity than did non-invasive species but

that it was only sometimes associated with fitness benefits. Compared to invasive species, indigenous species were able to maintain better fitness homeostasis under resource-limited or other stressful conditions (DAVIDSON et al. 2011). CHOWN et al. (2007) found that, in springtails, it was the form rather than the extent of phenotypic plasticity that distinguished the responses of invasive and native species to climate change. Probably differences in the phenotypic plasticity play an important role in the climate change responses. *A. vulgaris* has a high degree of plasticity in its thermal biology and can quickly adjust its growth to temperature changes. Focusing on two traits (egg production and survivorship), KNOP & REUSSER (2012) compared three hypotheses relating fitness to phenotypic plasticity in *A. vulgaris* and *A. fuscus* (O. F. Müller, 1774), which differ in many respects (e.g. habitat preferences, relationship). The first hypothesis was that the slugs would maintain fitness in stressful environments (the "robust" hypothesis). The second was that they would increase fitness in favourable environments (the "opportunistic" hypothesis). The third was that the slugs would be both "robust" and "opportunistic". During summer, *A. vulgaris* displayed a more adaptive phenotypic plasticity: when temperatures were high and food supply small, it survived better and produced more eggs than *A. fuscus*, which had adopted the robust phenotype. During winter, it was *A. fuscus* that had the more adaptive phenotype (KNOP & REUSSER 2012). These results indicate that *A. vulgaris* is robust and that warmer summers and milder winters might allow it to reach higher altitudes and spread further into the lowlands, which supports the worry that climate change may facilitate biological invasions (KNOP & REUSSER 2012). So far this is the only study that compares hypotheses relating fitness to phenotypic plasticity in *A. vulgaris* and another *Arion* species.

The reason for the mass occurrences and consequent pest status of *A. vulgaris* remains obscure, but some reports state that the species' success is related to its superior resistance to natural stresses such as drought and low winter temperatures, and that in this way it may outcompete its closely related congeners. SLOTSBO et al. (2012) compared cold tolerance in three *Arion* species (*A. ater*, *A. rufus* and *A. vulgaris*) in Denmark, but did not find any significant difference, further challenging the notion that *A. vulgaris* had a higher cold tolerance. Drought tolerance is another important factor that might influence its success. However, SLOTSBO et al. (2011) found that juveniles and eggs of *A. vulgaris* had a water loss rate and tolerance similar to those of other slug species. Gastropods generally have a relatively high water loss tolerance, and for *A. vulgaris* the authors reported a mortality of 50% when losing 72% water for ju-

veniles and when losing 81% for eggs. Furthermore, they noted that drought generally limited foraging, slowed down development and thereby delayed reproduction.

#### ENEMY RELEASE HYPOTHESIS

According to the enemy release hypothesis (ERH) the lack of natural enemies in an invader's introduced range influences its abundance or impact (estimated using individual size, population abundance, or propensity to displace native species) (LEE 2002, TORCHIN et al. 2003, COLAUTTI et al. 2004). ROSS et al. (2010) compared the occurrence of parasites in 23 slug species (*Deroceras reticulatum*, *D. panormitanum*, *D. laeve*, *Arion ater*, *A. circumscriptus*, *A. distinctus*, *A. fasciatus*, *A. flagellus*, *A. hortensis*, *A. intermedius*, *A. lusitanicus*, *A. owenii*, *A. silvaticus*, *A. subfuscus*, *Arion* sp., *Limax flavus*, *L. marginatus*, *L. maximus*, *L. valentianus*, *Limax* sp., *Milax gagates*, *Tandonia budapestensis*, *T. sowerbyi*) in their native range in the UK and their introduced range in the USA, and found support for the ERH (ROSS et al. 2010). However, the situation may be somewhat more complex. COLAUTTI et al. (2004) suggested that there were strong, enemy-specific effects on host survival and that hosts developed tailored defences. It is the release from the specific enemy that causes direct changes to survivorship, fecundity, biomass, or demographic variables that matters. Indeed, it is of little consequence if a species escapes an enemy or enemies against which it is well defended (COLAUTTI et al. 2004). In a study of carabid beetle predation on *A. vulgaris* in Norway, HATTELAND (2010) found that the slug still faced natural enemies even in its introduced range. It was observed that *Pterostichus niger*, *P. melanarius*, *Carabus nemoralis*, *C. violaceus* and the staphylinid beetle *Staphylinus erythropterus* preyed on eggs and hatchlings of *A. vulgaris* (PAIL 2000, PAILL et al. 2002, HATTELAND et al. 2010, 2011). *Pterostichus* species are more restricted in the size of prey taken compared to larger and more specialised predators, such as *Carabus* spp. (HATTELAND et al. 2010). *C. nemoralis* was shown to be a potentially important predator of the alien *A. vulgaris* in spring and may contribute to conservation biological control (HATTELAND et al. 2011). This species killed and consumed juvenile slugs of up to one gram (HATTELAND 2010). However, in intensively farmed areas, predator populations may be reduced in size, leading to a greater abundance of *A. vulgaris*. Temperature can also affect rates of predation on slugs. The activity threshold of *C. nemoralis* is 4°C; the activity is greater when temperatures rise in spring, but is not correlated with temperature later in the season (HATTELAND et al. 2011).

The enemy release hypothesis may explain the high frequency of occurrence of *A. vulgaris* in the in-

vaded areas in the absence of natural enemies, but sometimes despite their presence the abundance of invasive species may be substantial due to the influence of different factors.

#### RAPID RESPONSE TO NATURAL SELECTION

A number of taxa demonstrate rapid rates of evolution, including species that have invaded new areas and native species confronting invasions (HOFFMANN & SGRÒ 2011). Consequently, natural populations may be able to use evolutionary adaptation to deal with rapid climate change. Moreover, accounting for evolution can greatly change predictions regarding colonisation patterns and distribution shifts (HOFFMANN & SGRÒ 2011).

SEITER & KINGSOLVER (2013) studied reaction norms for body size, development time, potential fecundity, and immune function in four populations of *Pieris rapae* (L., 1758), the invasive cabbage white butterfly; its populations were found at different latitudes. They showed that there was rapid evolutionary divergence along latitudinal gradients and geographical differentiation in development time. They also discovered that immune response and phenotypic plasticity were more closely related to latitudinal variation in season length and natural enemies than to variation in ambient temperatures (SEITER & KINGSOLVER 2013). It is important to note that native species can also adapt to environmental variation by evolving greater plasticity and that plasticity as well as trait values may vary along latitudinal gradients. In a different study, KINGSOLVER et al. (2007) showed that the temperature-size rule and the related thermal reaction norms could demonstrate rapid, within-species evolution under natural conditions.

STAMPS (2007) argued that selection for high individual growth rates would increase mean levels of risk-taking behaviour across populations. Similarly, a high population growth rate may further encourage dispersal. The high life-time productivity of *A. vulgaris* with over 400 eggs per individual may compensate for a higher mortality and at the same time allow rapid population growth in newly colonised locations (KAPPES et al. 2012). It was also confirmed that *A. vulgaris* was less sensitive to otherwise adverse stimuli, and thus more likely to utilize novel environments and otherwise unusual dispersal routes (SLOTSBO et al. 2011, KAPPES et al. 2012).

It is expected that species in which selection is against individuals taking dispersal-related risks under undisturbed conditions may acquire (or loose) traits and become successful invaders when the conditions change. *A. vulgaris* is a suitable organism for testing this hypothesis and dispersal behaviour which includes various traits, such as mobility and feeding activity, boldness, exploration, sociability





and aggressiveness (COTE et al. 2010, KAPPES et al. 2012).

#### CLIMATE CHANGE

When discussing species invasions, one issue that can not be overlooked is climate change. Changing global conditions influence the distribution of native species and facilitate the spread of invaders (JANION et al. 2010, PELTANOVÁ et al. 2011). Climate change is clearly one of the most important factors affecting the distribution of all species. Species that stand to benefit from climate change will have certain traits that are well suited to the new conditions. There were two major peaks in invertebrate expansions. They took place in the 1950s and 1990s as a result of climate warming and habitat degradation (RABITSCH 2008, PELTANOVÁ et al. 2011). Many studies indicate that numerous species shifted their ranges towards the poles – towards higher latitudes – because of changes in temperature and precipitation (RABITSCH 2008, PELTANOVÁ et al. 2011, BEBBER et al. 2013). The rapid spread of pest or invasive species through increases in latitudinal range may have resulted either from the direct effects of climate change or from the intensification of foreign trade over the past six decades, meaning synergies are at play (PELTANOVÁ et al. 2011, BEBBER et al. 2013).

Climate conditions shape the distribution of *A. vulgaris*. KROCHMAL-MARCZAK et al. (2013) estimated the threat to plants by *A. vulgaris* in a field study in Żywnów (south-eastern Poland), taking into account the climate conditions of the region. Mild winters and substantial spring and autumn rainfall promoted the species' growth and expansion. The largest increase in *A. vulgaris* was observed during a year with a large rainfall in June and July, and the smallest increase was associated with an abnormal-

ly low rainfall in April, May, August, and September. Recently, *A. vulgaris* was more prominent in areas that had experienced frequent and periodic flooding (e.g. south-eastern Poland) (KROCHMAL-MARCZAK et al. 2013).

In Norway, geoclimatic parameters such as average monthly temperature and precipitation, were used to describe a potential future distribution of *A. vulgaris* in this country. The study revealed that large parts of coastal and lowland Norway would be potentially suitable areas for this pest (HATTELAND et al. 2013). The results showed that *A. vulgaris* was clearly favoured by the mild and wet Atlantic climate of the western coast. The damage reported in gardens and horticulture (e.g. strawberries) related to this pest was especially pronounced in coastal areas. It can be expected that habitat structure and its resulting micro-climate may be more important for the establishment of populations of *A. vulgaris*. Moreover, regardless of regional differences, precipitation throughout the whole country was not a limiting factor for *A. vulgaris* (HATTELAND et al. 2013).

As mentioned above, *A. vulgaris* is spreading from central to northern Europe. PELTANOVÁ et al. (2011) found that, over the last 30 years, the number of non-native land snail species found outdoors in the Czech Republic had increased from 5 to 15 (8% of all species). More than half of these were presumed to have originated in the Mediterranean, suggesting an influx of terrestrial invertebrates from more southerly regions (the so-called “Mediterranisation”; RABITSCH 2008, PELTANOVÁ et al. 2011). Although gastropods are known to have limited abilities of active dispersal, some dramatic, human-facilitated range expansions have recently been observed in Europe (PELTANOVÁ et al. 2011). However, they would have been more limited in scope if not for the changing climatic conditions.

#### THE CASE OF ARION VULGARIS

*A. vulgaris*, together with its congeners, for example *A. distinctus*, *A. fasciatus*, *A. flagellus*, *A. silvaticus*, is an invasive species which has recently become established in many European countries and is regarded as a serious pest, both in agricultural crops and in gardens (KOZŁOWSKI et al. 2010). The population size of *A. vulgaris* can vary substantially between years, likely due to climatic factors such as temperature and precipitation. Its growth, egg developmental time and hatching success are influenced by temperature. Increase in temperature below 25°C results in an increase in growth rate. *A. vulgaris* has a high degree of plasticity in its thermal biology and can quickly adjust its growth to temperature changes (SLOTSBO 2012). However, all factors potentially

contributing to the species' invasiveness should be examined.

Both juveniles and adults of *A. vulgaris* are freeze-tolerant, but only at relatively high sub-zero temperatures (–2°C). Both may survive in a super-cooled state, but are generally poor super-coolers. Therefore, the winter survival of *A. vulgaris* in very cold regions to a high degree depends on using microhabitats protected from low winter temperatures. Like other slugs, *A. vulgaris* has little resistance to evaporation, but on the other hand it tolerates rather substantial water loss. Its eggs are slightly more tolerant to water loss than are the juveniles. The development time of the eggs was found to increase with increasing desiccation because embryonic develop-

ment is stopped by dehydration. Despite tolerance of substantial water loss, *A. vulgaris* depends on moist habitats.

Besides the effects of climatic conditions, biotic factors such as predation, or competition with other slug species for food and space, may also affect the population dynamics of *A. vulgaris*. Moreover, it has to be borne in mind that the species is still being unintentionally dispersed between regions due to human activity (SLOTSBO 2012).

The Spanish slug's origin and taxonomy are somewhat unclear, which might be the result of rapid evolutionary changes having taken place during its range expansion. For this reason, broad-scale phylogeographic research, such as that conducted by PFENNINGER et al. (2014), should be carried out in the future. Using statistical phylogeography (drawing on mitochondrial and nuclear markers) and species distribution models, PFENNINGER et al. (2014) found that the Spanish slug was very probably native to central Europe and not an invader. They tested a variety of hypotheses: that introduced individuals of *A. vulgaris* had come from a few sites in its area of origin (western France or Spain), or that some specimens had been introduced at a few sites in the invaded range, and that the species is continuing to expand its range. They collected 300 individuals of *Arion* species from 60 localities in central and western Europe. The number of localities from each country ranged from 1 to 22; 22 localities in France and 12 in Spain. The maximum likelihood analysis

of the COI sequences defined 40 terminal clades; the average sequence divergence ranged from 3% to over 90%. Representatives of the *A. vulgaris* clade were found in France (northern and eastern regions), Germany, Austria, Switzerland, Slovenia, Denmark, Belgium, The Netherlands, and Luxembourg, but not in the presumed area of origin. Moreover, no haplotypes from Spain or western France co-occurred with haplotypes from central Europe. This result suggests that the slug tends to disperse passively and that the genus *Arion* tends towards invasiveness. It also shows that further research on the entire genus is needed, especially on integrative taxonomy. It was previously assumed that more than one introduction event had occurred and that most populations in the invaded range had experienced genetic bottlenecks (ENGELKE et al. 2011). This assumption needs to be revised. Furthermore, it is thought that *A. vulgaris* hybridises with *A. ater* and *A. rufus* (ROTH et al. 2012, DREIJERS et al. 2013), which could also have an influence on its invasiveness and expansion patterns. It was also suggested that hybridisation resulted in *A. rufus* disappearing from the areas invaded by *A. vulgaris* (DREIJERS et al. 2013). However, ALLGAIER (2015) failed to confirm hybridisation between *A. lusitanicus* and *A. rufus* in the field which may be due to different habitats. JONES et al. (2013) found that the establishment probability of non-native species declined with phylogenetic distance, which means that the presence of close relatives may have helped the Spanish slug establish itself (JONES et al. 2013).

## CONCLUSIONS AND FUTURE DIRECTIONS

There are many interdependencies among biological invasions, climate changes, and genomics (CHOWN et al. 2014). Climate change facilitates biological invasions in natural communities, which, in turn, can cause changes to natural environment. Also, arrival of an invasive species creates opportunities for hybridisation and introgression, which can be observed in natural habitats and have effects on biodiversity. There are many genomic tools that can shed light on the invasion-associated risks and thus can be used in monitoring of management strategies. These tools include metabarcoding, metagenomics, and analysis of entire genomes or genomic markers (CHOWN et al. 2014). Metabarcoding and metagenomics are ways of monitoring certain communities where climate changes facilitate the appearance of invasive species. Moreover, whole genome analysis can be used to track hybridisation and introgression as changes in certain genome areas are followed. Genomic markers make it possible to ascertain the origin of invasive species and to examine patterns of their range expansion.

The knowledge of behavioural differences between invasive and native species is thus crucial for a better understanding of the mechanisms underlying invasion success and to predict the spread of invasive species (KAPPES et al. 2012). There are many hypotheses regarding the causes of species invasiveness. In the case of *A. vulgaris*, a serious pest species, understanding of the mechanisms underlying its success is crucial. Moreover, the story of its expansion is unusual, and studying it in greater detail could considerably expand the knowledge of invasiveness, ecological patterns along latitudinal clines, and adaptations to novel environments. As observed by SEITER & KINGSOLVER (2013) "biotic invasions are natural experimental systems for studying the rapid evolution of traits and plasticity". Their argument is that novel environments place strong selection pressure on invasive species, resulting in new adaptations (SEITER & KINGSOLVER 2013). In the future, more emphasis should be placed on comparing the life-history traits and phenotypic plasticity of *A. vulgaris* with those of native species. Differences among *A. vulgaris*, *A.*





ater, and *A. rufus* populations found at various latitudes could help explain the rapid expansion of *A. vulgaris*. Combining broad-scale molecular and phylogeographic research with morphological studies could help decipher the taxonomy of *A. vulgaris* and its distribution pattern in its native range. Research on the species' natural enemies could also clarify its evolutionary history. Moreover, the influence of climate change on its distribution patterns should be explored because recent discoveries indicate that its

biogeographical history may be very complicated and interesting.

#### ACKNOWLEDGEMENTS

This work was supported by grants from the Polish-Norwegian Scientific Cooperation (Pol-Nor/201888/77) and from the Jagiellonian University (DS/WBINOZ/INOŚ/747).

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- Received: February 8th, 2016*  
*Revised: April 21st, June 9th, December 14th, 2016, March 3rd, 2017*  
*Accepted: April 3rd, 2017*  
*Published on-line: May 22nd, 2017*

