

Differences in field behavior between native gastropods and the fast-spreading invader *Arion lusitanicus* auct. non MABILLE

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ABSTRACT. Dispersal is a crucial process for population exchange and expansion, and traits that facilitate dispersal may be positively selected during biological invasions. Here, we performed a basic study on differences in behavior between the slug *Arion lusitanicus* auct. non MABILLE, 1868 (Gastropoda: Pulmonata), which is considered to be one of the 100 worst invasive species in Europe, and native gastropods. We assumed that the species is more active and less sensitive to otherwise aversive stimuli, and thus more likely to utilize novel environments. We quantified field densities and performed pitfall trap studies in 15 differently-structured habitats (urban, grassland, succession, riverine forest) in the floodplain of the LTER (Long Term Ecological Research) site 'Rhine-Main-Observatory' in Hesse, Germany. Here, *A. lusitanicus* was naturalized and scored 15 in terms of abundance rank, but was the dominant species in terms of trappability with the acidic Renner solution. A more detailed approach with a set of different baits showed that individuals of the invader were attracted to the acidic Renner solution, mustard oil, and garlic extract, all of which the native snails and slugs avoided. The results support the hypothesis that the invasive slug differs from other gastropods in its behavioral response to unusual, novel stimuli that may indicate some potential threat to other gastropod species. Future studies are needed to show if this behavior is related to personality traits such as exploration, boldness and risk-taking, and if it may have been positively selected in the context of the slug being passively spread in severely-transformed habitats such as gardens and greenhouses.

KEY WORDS. behavioral ecology, non-native organisms, dietary conservatism, foraging, trap efficiency

INTRODUCTION

Dispersal and colonization success are the drivers for gene flow and population dynamics in the metapopulation framework, and among the main issues in restoration ecology and invasion biology (BOWLER & BENTON, 2005). Dispersal creates a spatial response to environmental changes. An increase in dispersal ability can reduce losses otherwise associated with reaching distant resources. Indeed, it has been noted that individuals at the dispersal front differ from those of well-established or only slowly expanding populations in morphology (e.g. PHILLIPS et al., 2006; HASSALL et al., 2009) and in behavior (e.g. ALFORD et al., 2009). Similarly, individuals from invasive species differ from

those of non-invasive species in their dispersal-related behavior (e.g. SCHÖPF REHAGE & SIH, 2004; COTE et al., 2010).

Knowledge of behavioral 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. However, studies on dispersal-related behavior have so far focused on fast-moving vertebrates or arthropods. Yet, there are several highly successful slow-moving invaders that may serve as models for the study of dispersal-related behavioral traits. For example, the Lusitanian slug *Arion lusitanicus* auct. non MABILLE, 1868 (in some publications syn. *A. vulgaris* MOQUIN-TANDON, 1855) scores

among the 100 worst invasive pest species in Europe (DAISIE, 2010). The species probably originates from SW Europe, has been spread over large parts of the rest of Europe during the last decades (KOZŁOWSKI, 2007), and has also been introduced to the USA (DAISIE, 2010). It has most likely been repeatedly introduced by ornamental plant trade (e.g. SCHMID, 1970), and rapidly spread thereafter. It is a notorious feeding generalist (e.g., BRUELHEIDE & SCHEIDEL, 1999; BRINER & FRANK, 1998; KOZŁOWSKI, 2007), displays high life-time productivity (KOZŁOWSKI, 2007) and is capable of self-fertilization (e.g. HAGNELL et al., 2006), although this is not its dominant mode of reproduction (ENGELKE et al., 2011). While eggs and juveniles are the main targets of beetle predation in the invaded range, the predators are obviously ineffective in controlling slug abundance (e.g. HATTELAND, 2010; HATTELAND et al., 2010).

Arion lusitanicus occurs on disturbed grounds and even in severely modified areas such as cities, suburbs and agricultural areas. In contrast, large close-canopy beech-dominated forests are scarcely invaded by the species (KAPPES, 2006; KAPPES et al., 2009). Among the characteristics of anthropogenic disturbance are artificial habitat structures (e.g. soil sealing, artefacts made from plastic and/or metal), different and novel food sources (e.g. human food waste, garden waste, introduced ornamental plants, fruits and crops, faeces of different animals), chemical modifications (e.g. liming, fertilization, plant and crop protection) and increased microclimatic amplitudes.

We thus hypothesized that individuals of *A. lusitanicus*, in contrast to native species, do not strictly avoid physicochemical modifications or unusual substances that in some cases can be exploited as food. We performed a field study using pitfall traps with different baits that should be either attractive (beer: EDWARDS, 1991), neutral (water during a period with intermittent rain), or repellent (strong acids, isothiocyanates: e.g. KOHN, 1961 and references therein; SAHLEY, 1990; INOUE et al., 2004, 2006) to gastropods. In

a novel approach, we assessed the behavior of *A. lusitanicus* against the background of all the gastropod species we found in different habitat types.

MATERIALS AND METHODS

Data collection

Pitfall traps are known not to measure the true abundances of species in the habitat (BAARS, 1979), but rather reflect behavioral differences between species (GERLACH et al., 2009). We thus used pitfall traps to compare the trappability of *A. lusitanicus* with that of other gastropod species. The opening of the pitfall traps was 5.5 cm in diameter and the traps were protected against rain with a transparent plastic roof.

In a first sampling campaign, we sampled four major habitat types, namely transformed open habitats close to urban areas ($n = 4$), extensively-used open grounds (herb stands and grasslands, $n = 3$), herb-rich successional habitats ($n = 4$), and floodplain forests ($n = 4$) along the Kinzig River in the area of the Long Term Ecological Research (LTER) site 'Rhine-Main-Observatory' (www.lter-d.ufz.de) in southern Hesse, Germany (Figure 1B). We additionally quantified gastropod densities in each of the 15 locations. To this end, we sampled vegetation, plant litter and soil from four plots per location covering 0.25 m² each. As the plots are rather small for larger species, we included gastropod species found within a buffer of 2 m from the plot. These additional species received a lower score according to their probability of crossing the plots (0.5 = alive, 0.1 = dead). Large individuals (> 2.5 cm) usually were quantified and released in the field; medium-sized and small slugs were sorted from the fresh substrate collections in the laboratory, and the remaining snails were finally sorted from the air-dried material under a magnifying lens. Some slugs, such as those from the *A. subfuscus* complex or those belonging to the genus *Deroceras*, were determined anatomically.

For this first sampling campaign, eight replicate pitfall traps per location were filled with 250 ml Renner solution (10 % glacial acetic acid, 20 % glycerin, 30 % ethanol, 40 % water). Gastropods usually do not respond to glycerin, but display a negative response to acids (KOHN, 1961, and references therein). Ethanol and ethyl acetate, the latter being the product of acetic acid and ethanol, are both adverse stimuli for *Helix pomatia* (VOSS, 2000). This solution thus allows the assessment of potential behavioral peculiarities, and the substances do not evaporate as quickly as, for example, mustard oil. Pitfall traps remained for three weeks in the field (late July to mid-August 2010) and were checked and recharged weekly.

In a second pitfall trap sampling campaign, we compared the responses to five different baits.

- (1) Some pitfall traps were filled with Renner solution.
- (2) In the same habitats, we also offered pitfall traps filled with Pilsner type beer (4.9% ethanol) as beer is attractive for snails and slugs (EDWARDS, 1991; SCHÜRSTEDT & GRUTTKE, 2000; MAZE, 2009).
- (3) Mustard oil (allyl-isothiocyanate, AITC) is a pungent secondary metabolite of several crucifer plants including mustard and horseradish, but isothiocyanates also occur in garlic. Slugs are naturally averse to these substances (SAHLEY, 1990; INOUE et al., 2004, 2006). We prepared an 800 μ M solution of AITC by dissolving 400 μ l in 8 ml methanol and adding this solution to 5 liters of water.
- (4) A garlic solution was prepared as a cold extract of 20 g of smashed garlic cloves in 5 liters of water.

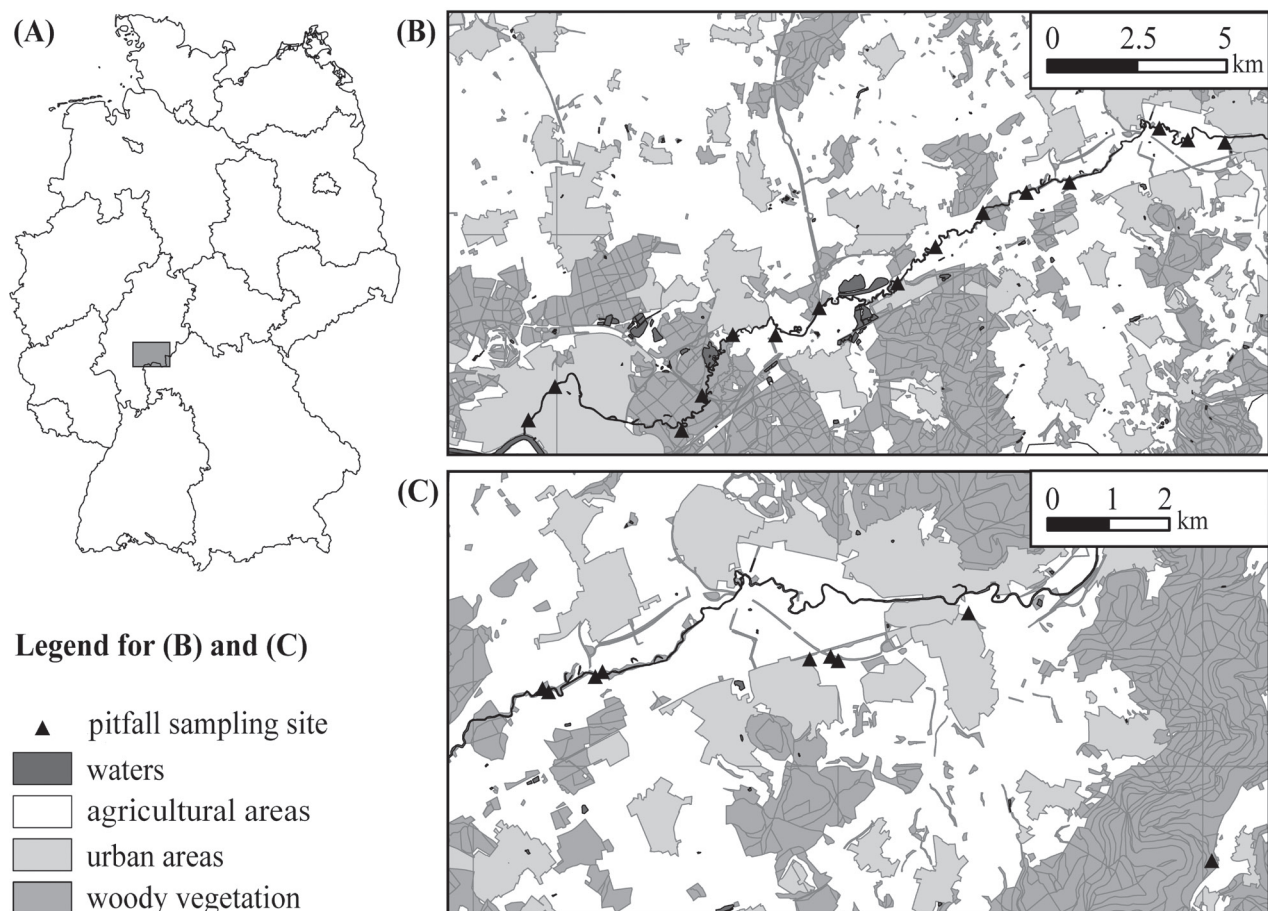


Fig. 1 – (A): Location of the survey area (shaded in grey) in the federal state of Hesse in Germany. (B): location of the pitfall traps in the sampling campaign with Renner solution. (C): location of the pitfall traps in the sampling campaign with the different baits. Where the pitfall trap locations were comparatively close in (C), contrasting habitat types were sampled.

(5) Water was considered to be neither deterrent nor attractive, because intermitted rainfall occurred throughout the study. Pitfall traps with water were thus used as a control for accidental drowning.

Two pitfall traps per bait type (250 ml) were placed in nine different locations (Fig. 1C) for five days during moist conditions in mid-August. The sampling was done in herb stands located along a railroad track (1x), at a drainage ditch (1x), between a poplar stand and a grain field (1x), around compost heaps in an allotment area (1x), in a small open floodplain close to a forest edge (1x), in a riparian willow stand (1x), along the edge between a grain field and grassland (2x) and between a grain field and a successional forest (1x). The traps were recharged after two days and removed after another three days. The catch from each interval was standardized to total numbers per bait (i.e., two traps) and 24 h.

Statistics

Trappability was calculated as the total number of individuals from the traps divided by the total number of individuals per m² from the field survey. High numbers thus indicate high attractiveness of the traps, whereas low numbers indicate avoidance behavior.

Abundance data were cubic root transformed. The data of the first sampling campaign were analyzed in a nested ANOVA with sites being nested in habitat types. Differences in the numbers of trapped *A. lusitanicus* between different habitat types were assessed using the Tukey HSD post-hoc test. Data from the second sampling campaign were analyzed in a one-way ANOVA with Tukey HSD post-hoc tests for differences between the efficiency of different bait types. Analyses were performed in JMP 4.0.

RESULTS

In the vegetation, leaf litter and soil surface samples taken in the ‘Rhine-Main-Observatory’,

a total of 49 gastropod species were recorded. *A. lusitanicus* was ranked 15 in abundance (Table 1) but was the dominant species in the pitfall traps with Renner solution ($n = 537$ individuals, trap selectivity = 19.53). Density and trappability of *A. lusitanicus* were not correlated ($r = 0.25$, $F_{1,13} = 0.89$, $P = 0.36$).

Only a few other species were caught in the pitfall traps with Renner solution, and their trap selectivity was lower. All traps combined yielded five individuals of *Arion rufus* (total number from squares: 1.0 / trap selectivity = 5.00), one *Arion silvaticus* (6.0 / 0.17), one *Deroceras reticulatum* (32.0 / 0.03), one *Deroceras panormitanum* (1.0 / 1.00), one *Limax maximus* (1.5 / 0.67), one *Fruticicola fruticum* (18.6 / 0.05) and two subadults of the genus *Cepaea* (54.1 / 0.04 for the two *Cepaea* species combined).

The activity density of *A. lusitanicus* was highest in successional habitats with young woody plants and herb cover (Fig. 2). The nested ANOVA revealed that both the habitat type ($df = 3$, $F = 5.1$, $P < 0.001$) and the sampling location ($df = 11$, $F = 18.6$, $P < 0.001$) significantly influenced activity densities of *A. lusitanicus*.

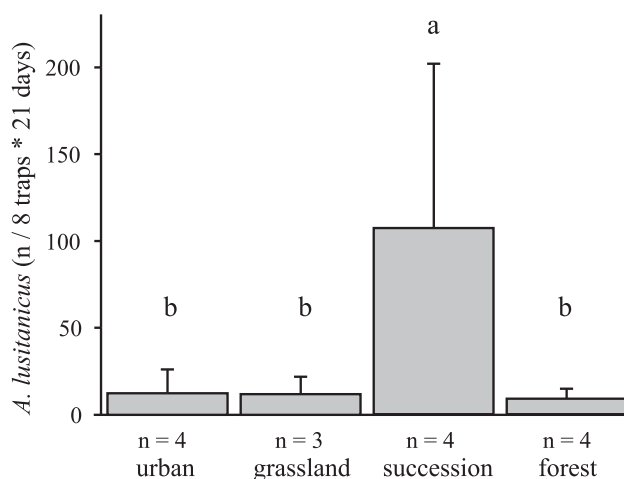


Fig. 2. – Differences between habitat classes in relation to the total catch of *Arion lusitanicus* (mean and standard deviation) in the eight pitfall traps (Renner solution) per location. Shared letters indicate a lack of significance for the Tukey HSD test in the nested ANOVA.

TABLE 1

Total numbers of individuals per 15 m² and average densities per m² of gastropod species of which more than 10 individuals were found in the 1 m² square survey in the 15 sites in the Rhine-Main-Observatory (compare Figure 1B).

species	total	mean±stdev. m ⁻²
<i>Cochlicopa lubrica</i> (O. F. MÜLLER, 1774)	480.5	60.1±53.5
<i>Alinda biplicata</i> (MONTAGU, 1803)	231.3	28.9±34.4
<i>Vertigo pygmaea</i> (DRAPARNAUD, 1801)	178.3	22.3±21.1
<i>Discus rotundatus</i> (O. F. MÜLLER, 1774)	79.7	10.0±7.2
<i>Punctum pygmaeum</i> (DRAPARNAUD, 1801)	63.2	7.9±8.4
<i>Carychium tridentatum</i> (RISSO, 1826)	55.5	6.9±5.1
<i>Acanthinula aculeata</i> (O. F. MÜLLER, 1774)	54.0	6.8±5.3
<i>Aegopinella nitidula</i> (DRAPARNAUD, 1805)	53.7	6.7±4.5
<i>Nesovitrea hammonis</i> (STRÖM, 1765)	49.9	6.2±3.9
<i>Cepaea hortensis</i> (O. F. MÜLLER, 1774)	39.1	4.9±2.8
<i>Trochulus hispidus</i> (LINNAEUS, 1758)	36.9	4.6±2.9
<i>Deroceras reticulatum</i> (O. F. MÜLLER, 1774)	32.0	4.0±1.5
<i>Monachoides incarnatus</i> (O. F. MÜLLER, 1744)	30.0	3.8±4.0
<i>Carychium minimum</i> O. F. MÜLLER, 1774	29.0	3.6±7.2
<i>Arion lusitanicus</i> auct. non MABILLE, 1868	27.5	3.4±1.3
<i>Succinella oblonga</i> (DRAPARNAUD, 1801)	24.9	3.1±4.0
<i>Vallonia excentrica</i> STERKI, 1893	22.7	2.8±2.7
<i>Vitrina pellucida</i> (O. F. MÜLLER, 1774)	22.1	2.8±3.3
<i>Vallonia costata</i> (O. F. MÜLLER, 1774)	20.9	2.6±3.4
<i>Fruticicola fruticum</i> (O. F. MÜLLER, 1774)	18.6	2.3±2.3
<i>Cepaea nemoralis</i> (LINNAEUS, 1758)	15.0	1.9±1.2
<i>Vertigo pusilla</i> O. F. MÜLLER, 1774	13.0	1.6±3.4
<i>Deroceras laeve</i> (O. F. MÜLLER, 1774)	12.5	1.6±0.9
<i>Succinea putris</i> (LINNAEUS, 1758)	11.2	1.4±1.3

A. lusitanicus was found in traps with all bait types in the choice experiment of the second sampling campaign. Individuals of *A. lusitanicus* were present in all traps irrespective of the bait, but the species was less well trapped with AITC and had a significantly lower constancy in traps with water ($P < 0.05$, Fig. 3A, Table 2). Based on the number of individuals of *A. lusitanicus*, bait types were ranked as follows: water < AITC < garlic extract < Renner solution < beer (Fig. 3B). Native species were rarely trapped; the most frequent native species was *D. reticulatum* (Table 2). Native species only occurred in the AITC, water and beer traps (in increasing order of total catch, Fig. 3A).

DISCUSSION

Density and activity

Our study revealed that *A. lusitanicus* differed from native species in having a higher overall trappability and a positive response to otherwise adverse substances. High activity of individuals of a species can cause a higher share of the species in pitfall traps than would be expected from field densities (BAARS, 1979), whereas a small movement range combined with specific microhabitat requirements may result in zero trappability, as we found for microsnails such as from the genera *Carychium*, *Punctum*, *Vertigo* and *Vallonia*.

TABLE 2

Gastropod catch from pitfall traps baited with beer, garlic solution, allyl-isothiocyanate (AITC) solution, Renner solution, and water in nine differently structured locations. Each bait type was offered in duplicate, thus mean and standard deviation are given per two traps and 24h.

species	beer	garlic	AITC	Renner	water
<i>Arion lusitanicus</i> auct. non MABILLE, 1868	10.37±5.03	1.05±1.08	0.31±0.30	2.23±2.17	0.08±0.13
<i>Arion fuscus</i> O.F. MÜLLER, 1774	0.02±0.07	-	-	-	-
<i>Arion silvaticus</i> LOHMANDER, 1937	0.04±0.13	-	-	-	-
<i>Arion distinctus</i> MABILLE, 1868	0.04±0.13	-	-	-	-
<i>Arion intermedius</i> (NORMAND, 1852)	0.09±0.20	-	-	-	-
<i>Deroceras leave</i> (O.F. MÜLLER, 1774)	0.19±0.22	-	-	-	0.02±0.07
<i>Deroceras reticulatum</i> (O.F. MÜLLER, 1774)	0.29±0.47	-	0.04±0.09	-	0.16±0.24
<i>Succinea putris</i> (LINNAEUS, 1758)	0.04±0.09	-	-	-	-
<i>Eucobresia diaphana</i> (DRAPARNAUD, 1805)	-	-	-	-	0.02±0.07
<i>Fruticicola fruticum</i> (O.F. MÜLLER, 1774)	0.02±0.07	-	-	-	-
<i>Monachoides incarnatus</i> (O. F. MÜLLER, 1774)	0.02±0.07	-	-	-	-
<i>Helix pomatia</i> LINNAEUS, 1758	-	-	0.02±0.07	-	-
<i>Cepaea hortensis</i> (O.F. MÜLLER, 1774)	-	-	0.02±0.07	-	-
<i>Cepaea nemoralis</i> (LINNAEUS, 1758)	0.04±0.13	-	-	-	-

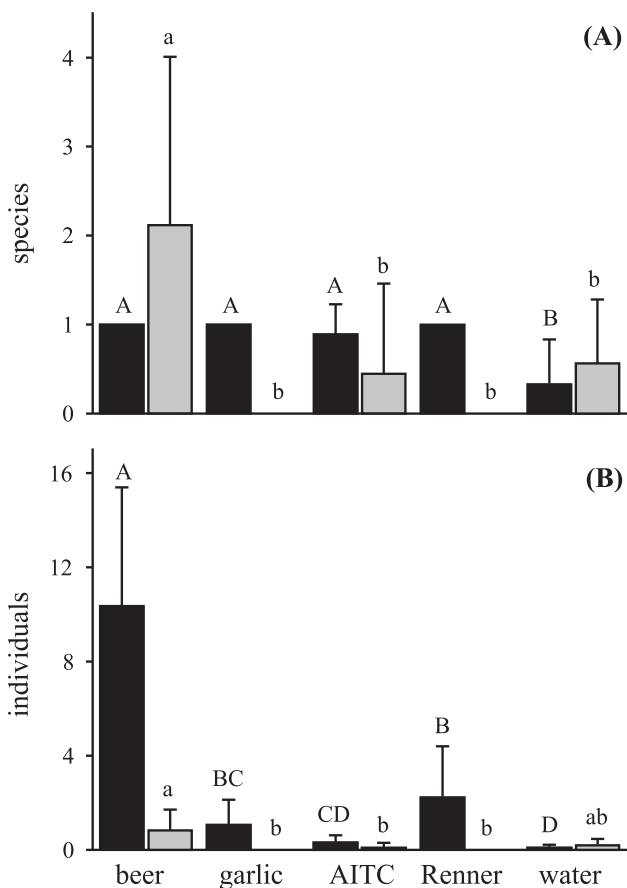


Fig. 3. – Mean and standard deviation of the total number of species (A) and number of individuals (B) trapped per bait type (two pitfall traps and 24 h) for all of the nine locations combined. Shared letters indicate a lack of significance in the Tukey HSD test. Black bars and capital letters refer to data of *Arion lusitanicus*, grey bars and small letters are for the native species.

Average field densities of *A. lusitanicus* in the habitats of the lower Kinzig valley were lower than, for example, those from herb-rich locations at the Lower River Rhine (KAPPES et al., 2007). Local densities can temporarily exceed 20 ind. m⁻² under optimal shelter and food conditions (KOZŁOWSKI, 2007, and references therein). Unlike many other gastropods, the individuals of this species seem to be gregarious, and many individuals can be found sharing the same shelter. The activity of *A. lusitanicus* is comparatively high. Individuals were found to move on average 10.8 m per night (GRIMM & SCHAUMBERGER, 2002), although great individual plasticity in activity and home range size was observed (GRIMM & PAILL, 2001). Thus, within this comparatively active species, some individuals may be even more likely than others to be involved in local spread.

Response to baits

Behavior towards pitfall traps is known to be influenced by the liquid in the trap. Beer is highly attractive to gastropods (SMITH & BOSWELL, 1970; SCHÜRSTEDT & GRUTTKE, 2000). In our study, the highest number of gastropod species was caught in beer traps. However, individuals from other species were outnumbered by *A. lusitanicus*, probably because of differences in exploring the trap with its potential food source. Similarly, the behavior at different stages of encountering pitfall traps differs greatly between soil arthropod species that display different trappabilities (GERLACH et al., 2009).

In contrast to the positive response to beer, most gastropods are known to show negative reactions to acids (KOHN, 1961; VOSS, 2000) and isothiocyanates (SAHLEY, 1990; INOUE et al., 2004, 2006). Our study confirmed that most gastropods except *A. lusitanicus* avoid solutions with these substances. Perception of the pungent components of garlic is modulated through the thermosensitive TRP (transient receptor potential) family of ion channels (JORDT et al., 2004; BAUTISTA et al., 2005). TRP channels occur throughout the animal kingdom although

the actual response to heat or cold depends on the taxon (e.g. VISWANATH et al., 2003). It has yet to be determined whether *A. lusitanicus* differs from the other gastropods in its perception of isothiocyanates.

Avoidance of acids reduces the risk of internal depletion of base cations and the associated reduction in fitness. Calcium salts, among others, are needed for shell growth and reproduction (WÄREBORN, 1979; TOMPA, 1976). Even though some species of the genus *Arion* have a strongly reduced internal shell, the egg shell of large *Arion* species, among them *A. lusitanicus*, is calcified or at least partially calcified (TOMPA, 1976). This lack of avoidance behavior towards acidic substances is in line with the observation that *A. lusitanicus* readily tests and feeds on plant species that contain oxalic acid such as the yellow wood sorrel (e.g. GRIMM et al., 1997) and the invasive giant knotweed (KAPPES et al., 2007). However, in our studies, attractiveness of the acidic Renner solution could not have been based on previous experience, as the habitats were dominated by *Urtica* stands, which typically do not provide strongly acidic food items. Instead, leaves of *Urtica dioica* are of neutral pH value (KAPPES et al., 2007).

Dispersal-related traits

Behavior can be discussed in terms of personality, that is, traits that are quite stable over time, that are heritable and that influence decisions of individuals within species (e.g. COTE et al., 2010). This can cause difficulties when describing the behavior of less-studied taxonomic groups or when comparing different taxa. Nevertheless, average levels of activity and exploration have, for example, been shown to differ between related invasive and non-invasive *Gambusia* shrimp species (SCHÖPF REHAGE & SIH, 2004). Exploratory behavior and novelty-seeking allow adaptation of the individual foraging strategy to spatio-temporal changes in food supplies (HARFMANN & PETREN, 2008; VAN OVERVELD & MATTHYSEN, 2010).

Among the risks of exploration is a higher mortality rate (e.g. STAMPS, 2007; BOON et al., 2008). Novel food items and situations can pose risks that often are overcome by dietary or behavioral conservatism; in our study this conservatism probably applied to most individuals of the active and abundant, but poorly trapped native *Deroceras reticulatum*. The high life-time productivity of *A. lusitanicus* with over 400 eggs laid by a single individual (KOZŁOWSKI, 2007) may be a strategy to compensate for a higher mortality and at the same time allow rapid population growth in newly colonized locations. STAMPS (2007) argued that selection for high individual growth rates would increase mean levels of risk-taking behavior across populations. Similarly, a high population growth rate may further encourage dispersal.

It is a much-debated question whether traits that favor dispersal or invasibility of their carriers were already common in populations in their native distribution range, or whether such traits are based on a rare genotype or even a single mutation that was positively selected for in the spreading process. *Arion lusitanicus*, for example, is very tolerant to, though not able to prevent, water loss (SLOTSBO et al., 2011). Our results, along with those of SLOTSBO et al. (2011) confirm that the species is less sensitive to otherwise aversive stimuli, and thus more likely to utilize novel environments and otherwise unusual dispersal routes. If a specific dispersal route is connected with some environmental stressors, for example high evaporation rates or chemical exposure, and some less sensitive genotypes can successfully overcome the stressors and colonize new areas, they will be selected for as long as the specific active or passive dispersal route persists, and in turn reinforce the use of the specific dispersal route.

We consequently expect that many more species, in which selection is against individuals taking dispersal-related risks under undisturbed conditions, may acquire (or lose) traits and become successful invaders under changing environmental conditions. Invasive

pest slugs such as *A. lusitanicus* would be highly suitable organisms for testing this hypothesis and dispersal behavioral syndromes, which, according to COTE et al. (2010), include traits such as locomotor and feeding activity, boldness, exploration, sociability and aggressiveness. In suggesting this, we would like to stimulate more research on the biology and behavioral plasticity of *A. lusitanicus* in its original distribution range, in areas where the species is already well established, and at the recent dispersal front(s).

CONCLUSION

The invasive slug species *A. lusitanicus* differs from native gastropods in terms of its active behavior, combined with some insensitivity or inertness to stimuli that usually are adverse for gastropods. High reproductive output (a buffer against losses from mortality), combined with these dispersal-related traits, can facilitate colonization and thus the invasiveness of the species.

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