Locomotor activity of two sympatric slugs: implications for the invasion success of terrestrial invertebrates

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Abstract. A central focus of invasion biology is to identify the traits that predict which introduced species will become invasive. Behavioral traits related to locomotor activity most likely play a pivotal role in determining a species' invasion success but have rarely been studied, particularly in terrestrial invertebrates. Here, we experimentally investigated the small-scale locomotor activity of two slug species with divergent invasion success in Europe, the highly invasive slug, *Arion lusitanicus*, and the closely related, non-invasive and native slug, *Arion rufus*. To do so, we used a multi-state capture-mark-recapture approach, and hypothesized that the invasive slug has a higher moving rate (keeps on moving) and leaving rate (leaves more frequently known places). A total of 221 invasive and 241 non-invasive slugs were individually marked using magnetic transponders and released in three study sites differing in habitat type. The slugs were recaptured using shelter traps, and moving and leaving rates were estimated. Both rates were significantly higher for the invasive slug, demonstrating a higher locomotor activity which might partly explain its invasion success. Our results provide evidence for the recently suggested idea that locomotor activity might be an important trait underlying animal invasions using for the first time terrestrial invertebrates.

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INTRODUCTION

To become invasive an introduced species must pass successfully through a series of stages such as transport, introduction, establishment and spread (Blackburn et al. 2011). Behavioral traits can be key factors for introduced species to survive the invasion process (Holway and Suarez 1999, Chapple et al. 2012). Specific behavioral traits might be crucial in various stages whereas others are only required during one stage (Chapple et al. 2012). As a consequence, successful invaders might be characterized by a suite of correlated behavioral traits (Sih et al. 2012), also known from behavioral ecology as behavioral syndrome (Sih et al. 2004).

Activity and boldness, for example, seem to be traits correlated in invasive species, possibly because they are important for all stages of the invasion process except the transit phase (Chapple et al. 2012). For example, Cote et al. (2010) showed for the invasive mosquito fish (*Gambusia affinis*) released in a novel environment that boldness, exploration and activity are behavioral traits which are positively correlated with each possibly explaining the invasiveness of the fish. Also, Pintor and Sih (2009) showed a positive relationship between invasive crayfish densities, aggression, and foraging activity, and they therefore postulate an aggression syndrome of

invasive species. These studies show that activity seems to be a crucial characteristic of behavioral syndromes of invasive species. However, invasion studies explicitly addressing activity remain scarce, and to our knowledge none of them used a terrestrial invertebrate as model organism.

Worldwide, many gastropods are listed as being invasive species (www.invasive.org). In Europe, the slug *Arion lusitanicus* (Mabille 1868) is highly invasive and thus listed as one of the hundred most invasive alien species in Europe (Rabitsch 2009). In Switzerland, first records of *A. lusitanicus* date back to the year 1950 (CSCF 2011). Since then, this species has successfully invaded all lowland parts of Switzerland (Turner et al. 1998). Concurrent with the invasion of *A. lusitanicus*, the native and formerly widespread *Arion rufus* (Linnaeus 1758) started to decline and to date only few small populations are left in the Swiss lowlands (Turner et al. 1998). *Arion rufus* is ecologically and morphologically similar to *A. lusitanicus*. The two species are only unambiguously distinguishable from each other by genetic means or by differences in the color patterns during juvenile stages (Bogon 1990, Quinteiro et al. 2005).

Here we investigated for the first time the locomotor activity of the two slug species, one a successful invader in Switzerland and the other not, using a multi-state capture-mark-recapture approach (Calvert et al. 2009). We placed tagged individuals of both species in a novel environment to investigate the following hypotheses: the invasive slug shows (1) a higher endurance to move around (keeps on moving, referred to as moving rate) and (2) a more pronounced exploratory behavior (leaves more frequently known places, referred to as leaving rate). Since movement behavior is often dependent on the matrix (Ricketts 2001, Prevedello and Vieira 2010), the study was conducted in three different habitats. The results highlight how locomotor activity might be associated with invasion success in a novel environment.

MATERIAL AND METHODS

Study site

The study was conducted in three sites near Uettligen, Switzerland (7°23′ E, 46°59′ N): a sown wild flower area, a pasture, and a stubble field. The sown wild flower area had been converted from arable land four years ago using a seed mixture of species characteristic for the region. The most abundant plant species on it were *Achillea millefolium*, *Centaura cyanus*, *Dactylis glomerata*, *Dipsacus fullonum*, *Festuca pratensis*, *Leucanthemum vulgare*, *Origanum vulgare*, *Phleum pratense*, *Poa trivialis*, and *Verbascum densifloruum*. The stubble field had been cultivated with wheat and harvested a week prior to the start of the experiment so that it was mostly covered with dead plant material and bare ground. Finally, on the pasture the most abundant plant species were *Dactylis glomerata*, *Poa trivialis*, *Taraxacum officinale*, and *Trifolum pratense*.

Study specimens

As only small populations of *A. rufus* are left in the Swiss lowlands (Turner et al. 1998), the specimens of *A. rufus* were taken from a colony described by Ryser et al. (2011). *Arion lusitanicus* were collected in a village in the lowlands of Switzerland (7°35′ E, 47°05′ N). The two slugs are difficult to distinguish by external means. However, juvenile specimens of *A. lusitanicus* have black stripes while *A. rufus* has not. We thus sampled specimens of *A. lusitanicus* in a stage when we still could detect the stripes. In addition, *A. rufus* has disappeared from the Swiss lowland and is currently only found at a few places in forests further reducing the likelihood to have collected *A. rufus*. Based on the results of a previous study showing that there is no difference in the survival of captive bred and wild *A. lusitanicus*, we assume that there was also no such difference in our study (Ryser et al. 2011).

Experimental set-up

In July and August 2010, 221 individuals of *A. lusitanicus* and 241 individuals of *A. rufus* were individually marked according to the method described in detail in Ryser et al. (2011). Two types of transponders were used: Individuals larger than 3 g (234 individuals) were marked using sterile transponders of 1 cm length and 0.2 cm width (Five-Star-ID-ISO-transponders from Esstra-microchips). Individuals between 2 g and 3 g (228 individuals) were marked using transponder of 0.9 cm length and 0.1 cm width (ID-fix Transponder from ufamed AG), sterilized

with 70% ethanol.

On each of the three fields a total of 121 shelter traps were placed 2.5 m apart from each other in all directions, starting from the center of the field, and resulting in three observation areas of 27.75 × 27.75 m (each 11 lines, 11 rows). The shelter traps (25 × 25 × 3 cm) were made from raw pinewood and were used to recapture the slugs by laying them on the ground. On 11 August 2010, a total of 408 individually marked slugs (187 specimens of *A. rufus*, 221 specimens of *A. lusitanicus*) were released under the central 12 shelters of each observation area resulting in 5–6 specimens of *A. rufus* per shelter trap, 6–7 of *A. lusitanicus*, respectively. On 24 August 2010, 54 additional *A. rufus* which were still too small for tagging at the beginning of the experiment were released under the central 9 plates of each site. From 12 August 2010 to 20 September 2010 the shelters were checked for marked slugs on five consecutive days per week, and the position and identity of the recaptured slugs were noted. The survey always started at 3.00 pm in a random-ized order.

Statistical analysis

To estimate the movement rates of the slugs, we applied a Cormack-Jolly-Seber (CJS) multi-state mark-recapture modeling approach (Cal-vert et al. 2009) using the software package MARK 5.1. This approach enables separate estimation of survival probabilities, encounter probabilities (the probability for encountering a living individual when searching for it), and transition probabilities between different states of different locomotion behaviors. Analyses were based on individual encounter histories (i.e., individual sequences of data reporting whether an individual was not found, found under the same plate as before, or found under a new plate), including 26 encounter occasions (i.e., 26 survey events checking encounter and location of individuals) over a period of 40 days. These encounter occasions represented single elements of the encounter histories. As the periods from one to the next encounter occasion were not always equal (five consecutive days of control-ling followed by two days break), the relative length of the time interval was entered into the model, so that the model estimated standardized rates per 24 h. All encounter histories started with the day of release. The 54 *A. rufus* that were released in the second cohort experienced a reduced sampling period compared to the first cohort, since sampling stopped for all individuals at the same time. We controlled for this difference by setting the encounter probability of the second cohort to zero for the last 9 encounter occasions where they could not be encountered, because no sampling occurred in this period. Two states were defined in the individual encounter histo-ries: Individuals found under the same plate as at the last encounter were assigned to the encounter state "stay"; individuals found under a new plate were assigned to the encounter state "move" respectively. The incorporation of these two states allowed the estimation of state-specific survival and encounter probabilities (separate survival and encounter probabilities for the state "stay" and the state "move"), as well as four different state transition probabilities, either staying or leaving the current state: (1) leaving rate (Ψ leave): probability that a staying slug leaves the plate from one to the next occasion; (2) settlement rate (Ψ settle): probability that a moving slug stays at the same plate from one to the next occasion; (3) resting rate: probability that a staying slug stays at the same plate ($1 - \Psi$ leave); (4) moving rate: probability that a moving slug keeps moving ($1 - \Psi$ settle). Leaving and resting rates are thus quantitative measures of the propensity for activity and exploration, whereas settlement and moving rate are quanti-tative measures of the slug's endurance to move around. They thus can vary independently, i.e., a species might have a high moving rate but always returns to the same plate resulting in a low leaving rate.

A goodness-of-fit (GOF) test was performed using the software package U-CARE (Choquet et al. 2009). The GOF suggested an adjustment of the overdispersion factor ($\hat{c}$) to $\hat{c} = 1.531$ ($\chi^2 = 119.390$, P $= 0.002$). Model selection was based on the Akaike Information Criterion adjusted for small sample sizes (AICc; Burnham and Ander-son 2002) and on the $\hat{c}$-adjustment resulting in a quasi-likelihood corrected Akaike Information Criterion (QAICc; Burnham and Anderson 2002). The model with the smallest QAICc value was chosen to make inferences about the outcome of the release experiment.

Table 1. The ten top-ranked models selected by the corrected quasi-likelihood Akaike Information Criterion (QAICc).

No.	Model name	QAICc	ΔQAICc	Parameter	Qdeviance
1	Φ total$_{(hab)}$ p stay$_{(spec+hab)}$ p move$_{(spec+hab)}$ Ψ leave$_{(spec+hab)}$ Ψ settle$_{(spec+hab)}$	1805.62	0	19	753.90
2	Φ total$_{(spec+hab)}$ p stay$_{(spec+hab)}$ p move$_{(spec+hab)}$ Ψ leave$_{(spec+hab)}$ Ψ settle$_{(spec+hab)}$	1806.23	0.62	20	752.42
3	Φ total$_{(spec\times hab)}$ p stay$_{(spec+hab)}$ p move$_{(spec+hab)}$ Ψ leave$_{(spec+hab)}$ Ψ settle$_{(spec+hab)}$	1806.96	1.34	22	748.95
4	Φ total$_{(spec\times hab)}$ p stay$_{(spec+hab)}$ p move$_{(spec+hab)}$ Ψ leave$_{(spec)}$ Ψ settle$_{(spec)}$	1807.34	1.72	18	757.71
5	Φ total$_{(spec\times hab)}$ p stay$_{(spec\times hab)}$ p move$_{(spec\times hab)}$ Ψ leave$_{(spec)}$ Ψ settle$_{(spec)}$	1809.32	3.70	22	751.30
6	Φ total$_{(hab)}$ p stay$_{(spec+hab)}$ p move$_{(spec+hab)}$ Ψ leave$_{(spec)}$ Ψ settle$_{(spec)}$	1810.34	4.70	15	766.94
7	Φ total$_{(spec\times hab)}$ p stay$_{(spec\times hab)}$ p move$_{(spec\times hab)}$ Ψ leave$_{(spec+hab)}$ Ψ settle$_{(spec+hab)}$	1811.60	5.99	26	745.13
8	Φ total$_{(spec\times hab)}$ p stay$_{(spec+hab)}$ p move$_{(spec+hab)}$ Ψ leave$_{(spec\times hab)}$ Ψ settle$_{(spec\times hab)}$	1812.25	6.64	26	745.78
9	Φ total$_{(spec+hab)}$ p stay$_{(spec+hab)}$ p move$_{(spec+hab)}$ Ψ leave$_{(spec)}$ Ψ settle$_{(spec)}$	1812.40	6.78	16	766.93
10	Φ total$_{(hab)}$ p stay$_{(spec+hab)}$ p move$_{(spec+hab)}$ Ψ leave$_{(spec\times hab)}$ Ψ settle$_{(spec\times hab)}$	1813.08	7.47	23	752.96

Notes: ΔQAICc = Deviation of the Quasi-likelihood and corrected Akaike Information Criterion to the best model; ĉ = 1.531; Φ = survival model; p = encounter model; Ψ = transition model; Φ total = no difference between Φ stay and Φ move; spec = species (*A. lusitanicus*, *A. rufus*); hab = habitat (stubble field, sown wild flower area, pasture).

Candidate models

Models were selected with a hierarchic three-step approach. In a first step, we modeled factors affecting encounter probabilities while keeping the survival and transition parts of the model fixed (most parameterized; Φ stay$_{spec*hab}$, Φ move$_{spec*hab}$, Ψ leave$_{spec*hab}$, Ψ settle$_{spec*hab}$). Thereby, models including all combinations of an effect of species and habitat (including their interaction) on state-specific encounter probabilities (p) were built, leading to a maximum of 36 parameters. In a second step, the best six encounter models were chosen to model all combinations of state-specific survival probabilities (Φ). Accordingly, in a third step, the six best models were chosen to model transition probabilities (Ψ). This approach resulted in a total of 102 candidate models. Evaluation of the top models within a ΔQAIC < 2 was done by following the rule of parsimony and using the likelihood ratio test implemented in the software package MARK 5.1.

RESULTS

Four models showed a deviation of ΔQAICc < 2 to the best model (model 1–4; Table 1). These four models differed only in the survival and the transition model. For the survival model, model selection favored model 1 including only an effect of habitat on survival probability: the likelihood ratio test showed no differences between model 1, 2 and 3 (model 1 vs. 2: $\chi = 1.48$, df = 1, p = 0.22; model 1 vs. 3: $\chi = 4.95$, df = 3, p = 0.15; model 2 vs. 3: $\chi = 3.47$, df = 2, p = 0.18), and following the principle of parsimony model 1 was preferred over model 2 and 3. For the transition model, model selection favored the transition model including the additive effects of species and habitat (Ψ leave $_{(spec+hab)}$ Ψ settle $_{(spec+hab)}$; model 3 vs. 4: $\chi = 8.76$, df = 4, p = 0.07; model 1 vs. 6: $\chi = 13.04$, df = 4, p = 0.01; model 2 vs. 9: $\chi = 14.51$, df = 4, p < 0.01).
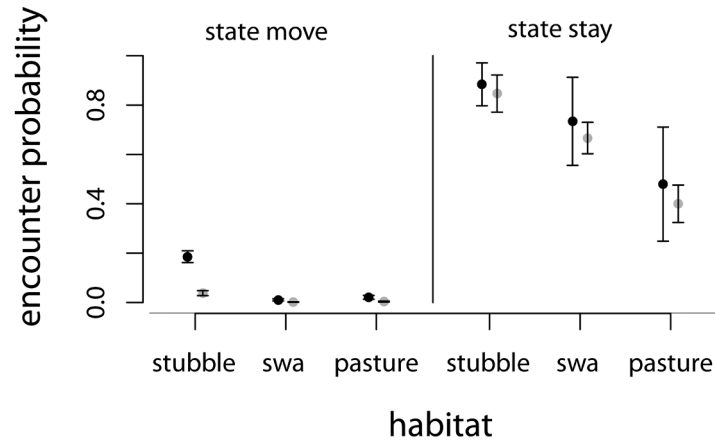
Survival probability Φ.—The local survival prob-

Fig. 1. Daily encounter probabilities. Daily encounter probabilities of the invasive slug *A. lusitanicus* (black; n = 221) and the non-invasive slug *A. rufus* (grey; n = 241) for the two states "stay" and "move" in the three different habitats (stubble field (stubble), sown wild flower area (swa), and pasture). Daily encounter probability was higher in the state "stay" for both species and in all habitats.

ability did not differ between the two states ("stay" or "move") in all ten top-ranked models, indicating that changing shelters did not affect survival rates, thus, dispersal costs being low. The best model indicated only a significant habitat effect on survival probability. The local survival was highest for both species in the sown wild flower area ($\Phi \pm SE = 0.96 \pm 0.03$), followed by the stubble field ($\Phi \pm SE = 0.92 \pm 0.01$), and the pasture ($\Phi \pm SE = 0.90 \pm 0.04$).

Encounter probability p.—The encounter probability of all ten top-ranked models differed significantly between the two states (Table 1) with a higher encounter probability in the state "stay", indicating that moving slugs showed lower encounter probability than staying slugs. The best model further revealed additive effects of habitat and species (Table 1) with the invasive slug *A. lusitanicus* having a higher encounter probability than *A. rufus* (Fig. 1). The encounter probability was highest in the stubble field (Fig. 1).

Transition probability Ψ.—While the moving rate ($1 - \Psi$ settle) was high and showed only small differences between the two species (higher for *A. lusitanicus*), the leaving rate (Ψ leave) was considerably higher for the invasive slug *A. lusitanicus* than for the native slug *A. rufus* (Fig. 2). This was true for all habitat types (Fig. 2). Leaving rate was lowest in the pasture whereas moving rate was lowest in the stubble

field (Fig. 2).

DISCUSSION

As expected the invasive slug *A. lusitanicus* showed a higher leaving and moving rate than the non-invasive slug *A. rufus*, demonstrating a higher locomotor activity in a novel environment. While this result is in line with previous studies showing a higher activity of invasive vertebrates or aquatic animals compared to non-invasive species (e.g., Petren and Case 1996, Rehage and Sih 2004, Pintor et al. 2008, Cote et al. 2010, Chapple et al. 2011), to our knowledge this is the first study to show this for a terrestrial invertebrate. Our result is supported by recent findings by Kappes et al. (2012) who used an indirect approach to measure the activity of *A. lusitanicus*: Compared to non-invasive mollusk species the invasive slug had a higher trapability when caught with pitfall traps indicating a higher activity. Thus, our study suggests that also in terrestrial invertebrates invasiveness might be associated with a high locomotor activity.

In invasive species, higher locomotor activity is often correlated with a suite of other behavioral traits, such as boldness, exploration, and foraging activity, and has been shown to lead to a higher resource exploitation (Pintor and Sih 2009, Cote et al. 2010). Higher resource exploitation usually
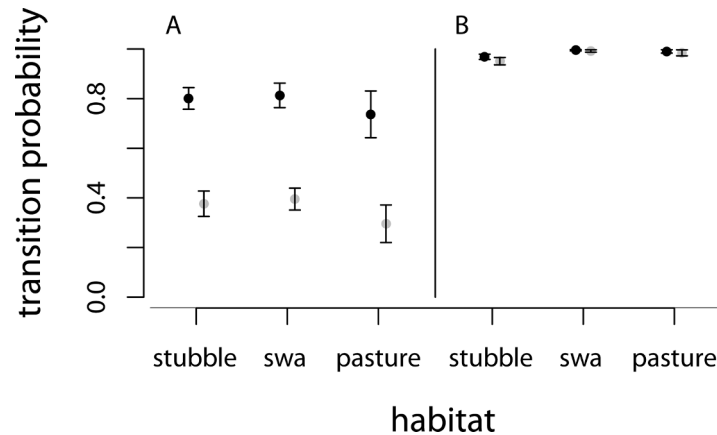
Fig. 2. Leaving rates (A) and moving rates (B). Leaving rates (transition probability from state stay to move) and moving rates (1 − the transition probability from state move to stay) of the invasive slug *A. lusitanicus* (black; n = 221) and the non-invasive slug *A. rufus* (grey; n = 241) in three different habitats: stubble field (stubble), sown wild flower area (swa), and pasture. The leaving and moving rate differed between the two species with higher rates for the invasive slug in all habitat types.

translates into higher fitness thereby providing a likely explanation for the superiority of invasive animals (e.g., see Petren and Case 1996, Byers 2000, Reitz and Trumble 2002, Pintor and Sih 2009).

In the context of habitat use, a higher locomotor activity could explain the superiority of *A. lusitanicus* compared to other mollusks. For example, the spatial flexibility might enable *A. lusitanicus* to cope more effectively with the intensively used and highly fragmented agricultural landscape of Central Europe thereby leading to a higher fitness. The underlying mechanisms might be twofold. On the one hand, on a local scale, frequent management disturbances are known to reduce mollusk densities (Voss et al. 1998). Being mobile enables to avoid such fatal management activities, e.g., feed on nutrient rich crop fields during night and avoid them during daytime when disturbances take place. Indeed, Honek and Martinkova (2010) showed that the invasive slug *A. lusitanicus* prefers to hide in dense stands of grass like the sown wild flower area from where it spreads into bordering fields or habitats for feeding. On the other hand, on a landscape scale, habitat fragmentation has been shown to negatively affect gastropod species (Gotmark et al. 2008, Kappes et al. 2009). In general, the strength of fragmentation effects depends on the mobility behavior of

the species (Ewers and Didham 2006). Moreover, within species, it has been shown that higher locomotor activity is associated with competitive dominance (Denardo and Sinervo 1994, Robson and Miles 2000, Perry et al. 2004). We suggest that this is also the case between species. Thus, a high locomotor activity, i.e., a high mobility, probably enables *A. lusitanicus* to perform better in a highly fragmented landscape compared to less mobile gastropods.

Here we studied the locomotor activity of two animal model organisms when released to a new location. We thus did neither consider earlier stages of the invasion process sensu Blackburn et al. (2011) (transport and introduction) nor did we investigate the exploration of a novel habitat at the invasion front. We found, however, that the invasive *A. lusitanicus* had consistently a higher locomotor activity than the non-invasive *A. rufus*, irrespective of the habitat type. This might indicate that the invasive slug performs well when facing novel environments. The habitat types did, however, differ regarding encounter probabilities with the highest encounter probability in the stubble field. This might be due to less opportunity for shelter in stubble fields without vegetation cover. However, further studies specifically addressing other stages of the invasion process are needed. For example, it has been shown that cane toads from the

dispersal front are morphologically adapted to move faster than conspecifics from well-established populations (Phillips et al. 2006). Further, they also differ in locomotor activity traits, which corresponds to the leaving rate in our gastropod study (Alford et al. 2009). A further research direction will be to address locomotor activity in concert with other behavioral traits in order to better characterize behavioral syndromes of invasive species, as for example the bold/exploratory/active syndrome postulated by Cote et al. (2010). We suggest that behavioral syndromes will turn out to be an important factor affecting invasiveness in animals, comparable with personality traits and behavioral syndromes in the context of animal dispersal (Clobert 2001, 2012).

Interestingly, populations of *A. rufus* have been declining in Switzerland whereas the species is invasive in USA. This could be due to advantages *A. rufus* has in its non-native range which the species does not have in its native range, such as release from nematodes as has been shown for several species of the genus Arion (Ross et al. 2010). In addition, it also could be that *A. rufus* belongs to a cryptic species complex which includes forms/species differing in their invasion potential as has recently been shown for the complex *Arion subfuscus/fuscus* (Pinceel et al. 2004). Analyses using genetic tools indicate the presence of cryptic species (unpublished data), but further analyses are needed to confirm this.

In summary, to our knowledge, this is the first study using a multi-state capture-mark-recapture approach to investigate spatial behavior of gastropods in the field. The higher leaving and moving rates of the invasive slug *A. lusitanicus* in all three habitats demonstrate a higher locomotor activity compared to the non-invasive slug *A. rufus*. How exactly this higher locomotor activity translates into invasion success is currently unknown, but recent studies suggest that the underlying mechanisms include increased resource exploitation and spatial advantages in the use of the intensively managed agricultural landscape (Honek and Martinkova 2010, Kappes et al. 2012). Our results provide evidence for the recently suggested idea that locomotor activity might be an important trait underlying animal invasions using for the first time terrestrial invertebrates.

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