



## Predation on invasive land gastropods by a Neotropical land planarian

Piter Kehoma Boll and Ana Maria Leal-Zanchet\*

*Instituto de Pesquisa de Planárias and Programa de Pós-Graduação em Biologia, Universidade do Vale do Rio dos Sinos – UNISINOS, São Leopoldo, Brazil*

(Received 22 May 2014; accepted 23 October 2014; first published online 18 December 2014)

Studies on the predatory behaviour of land planarians have focused mainly on established invasive species, while the feeding habits of non-invasive planarians are poorly understood. We analyse the predatory behaviour of *Obama ladislavii*, a land planarian native to southern Brazil that is common in both natural and human-disturbed areas. Observations were performed in the laboratory. Several groups of invertebrates were offered as possible prey and interactions between these invertebrates and planarians were recorded. *Obama ladislavii* fed on the introduced land gastropods *Bradybaena similaris*, *Helix aspersa* and *Deroceras laeve*, ignoring other invertebrates. Once potential prey were identified, we tested the ability of *O. ladislavii* to recognize and follow slime trails, and demonstrated the planarian's ability to follow chemical trails from prey in the environment. The consumption of exotic species indicates a flexible, generalist diet that is consistent with the ability of *O. ladislavii* to adapt to environments altered by human activities. Thus, this species may become invasive if introduced outside of its original distribution, but it also has the potential to be used in biological control programs for pest management in its native range.

**Keywords:** diet; Gastropoda; Geoplanidae; tracking; Tricladida

### Introduction

Land planarians are mainly predators and feed on other invertebrates such as slugs, snails, earthworms, woodlice, insect larvae, termites, springtails, other arthropods and even other land planarians. They are considered to be top predators in their microhabitats (Froehlich 1955; Barker 1989; Cumming 1995; Ogren 1995; Sluys 1998; Prasniski and Leal-Zanchet 2009), although a natural enemy of land flatworms was recently found in a subtropical ecosystem (Lemos et al. 2012). Prey capture methods vary among species, but include immobilization using slime and muscular movements (Froehlich 1955; Ogren 1995; Winsor et al. 2004; Ducey et al. 2007; Prasniski and Leal-Zanchet 2009). Some species may hunt in groups of several planarians and so capture large prey items (Barker 1989; Sugiura 2010) while others seem to be mainly scavengers (Winsor et al. 2004; McDonald and Jones 2014).

Most studies on predation by land planarians have focused on invasive species that pose possible threats to the stability of native ecosystems (Winsor 1983; Blackshaw 1990; Zaborski 2002; Sugiura et al. 2006; Murchie and Gordon 2013). Some of these species, e.g. *Arthurdendyus triangulatus* (Dendy), *Bipalium kewense* Moseley and *B. adventitium* Hyman, are known predators of earthworms. In addition, *Platydemus manokwari* De Beauchamp and *Endeavouria septemlineata*

---

\*Corresponding author. Email: [zanchet@unisinos.br](mailto:zanchet@unisinos.br)

(Hyman), which feed on land gastropods (Sugiura et al. 2006; Sugiura and Yamaura 2009), have also become threats. The success of these species outside of their native range is mainly due to their ability to feed on almost any species belonging to the same taxonomic group as their native prey. *Platydemus manokwari*, for example, has shown the capacity to feed on all species of snails offered to it (Kaneda et al. 1990). Such a generalist diet may allow these species to quickly disperse over newly invaded areas (Murchie et al. 2003).

The diet and behaviour of non-invasive land planarians have been neglected due to the planarians' fragility, which prioritizes specimen preservation for taxonomic studies (Ogren 1995). Furthermore, many species are difficult to keep under laboratory conditions due to the need to simulate their natural habitat and provide their preferential prey.

*Obama ladislavii* (Graff, 1899) is a common, native land planarian species in human-disturbed areas in the states of Rio Grande do Sul and Santa Catarina, southern Brazil (Graff 1899; Froehlich 1959), the climate of which is described as Cfa (temperate without dry season and hot summer) according to the Köppen-Geiger classification (Kottek et al. 2006; Peel et al. 2007). It can be found in both native and disturbed environments, in different forest formations, including seasonal and moist forests (Castro and Leal-Zanchet 2005; Fick et al. 2006; Antunes et al. 2008; Leal-Zanchet et al. 2011) as well as in urban and rural areas. It is easily recognized by its green coloration, and the largest specimens can be more than 100 mm long and 10 mm wide when extended (Graff 1899). We examined in the laboratory (1) the preferential prey items of *O. ladislavii*, and (2) its prey-tracking mechanism.

## Methods

### Collection and maintenance

Specimens of *Obama ladislavii* were collected under fallen logs, stones, leaves and flower pots in forests and gardens in Montenegro, São Francisco de Paula, and São Leopoldo, Rio Grande do Sul, Southern Brazil. The worms were kept individually in small terraria measuring  $13.0 \times 6.6 \times 3.5$  cm or  $9 \times 5.5 \times 2.6$  cm, depending on the size of the specimen. The terraria contained moist soil, leaves and log fragments to simulate the natural habitat of this species and were maintained in the dark under a temperature ranging between 18 and 20°C and a relative air humidity of about 90%.

### Prey preference and capture method

In the first experiment, several invertebrate species common in the range of the planarians were offered as potential prey items, namely gastropods: *Bradybaena similaris* (Férussac), *Helix aspersa* Müller, *Meghimatium pictum* (Stoliczka), *Deroceras laeve* (Müller, 1774) and *Happia* sp.; land isopods: *Atlantoscia floridana* (Van Name), *Balloniscus glaber* Araujo and Zardo, *Balloniscus sellowii* (Brandt), *Porcellio scaber* Latreille and *Armadillidium* sp.; termites: *Nasutitermes* sp.; earthworms: *Eisenia fetida* (Savigny), *Amyntas gracilis* (Rosa) and *Urobenus* sp.; land planarians: *E. septemlineata* and *Luteostriata abundans* (Graff, 1899); unidentified species of cockroaches, springtails, earwigs, millipedes and larvae of elaterid beetles.

In this experiment we used 25 specimens of *O. ladislavii*. The planarians were deprived of food for at least one week prior to the experiment and then fed once a week.

For the test, one (for gastropods, earthworms, planarians, cockroaches, earwigs, millipedes and elaterid larvae) or several (for isopods, termites and springtails) specimens of the potential prey item were placed in a moistened Petri dish together with the planarian and both predator and prey were induced to have physical contact with each other. The behaviour of the land planarian and the offered prey species were recorded.

If the planarian did not show any interest in the offered prey species or captured it without consuming it, one or several specimens of this potential prey were maintained for a week in the terrarium with the planarian to determine whether or not the rejection was caused by the artificial conditions of substrate and light in the Petri dish. If the planarian captured and consumed the offered prey, a different potential prey was offered one week later. The order in which different preys were offered to each planarian was random.

Data related to attempts and success of *O. ladislavii* in capturing prey were subjected to a chi-squared test by means of the program SPSS Statistics 19 (IBM Corporation, Somers, NY, USA) in order to determine whether there were statistically significant differences in the capture success of the several preyed upon items.

### ***Prey-tracking mechanism***

Once the prey species were known, a second experiment was performed to determine whether the planarians are able to track prey by following chemical signals left in the environment. In this experiment, we used 12 specimens of *O. ladislavii*. The method was adapted from the one used by Fiore et al. (2004).

In order to create a track of chemical signal, a specimen of one of the three prey species was placed over a layer of moistened filter paper inside a 14 cm diameter Petri dish and induced to move over it in a straight line across the diameter of the dish. The track was outlined with a pencil to make it visible (Figure 1). As a control, a track of moistened soil with approximately the same width as the slime track was created with a small brush over a filter paper in a different dish and also outlined with a pencil. The order of testing the planarians with slime or soil tracks was randomized. Each planarian was tested on either a slime or a soil track once a week and was fed right after the experiment, being then deprived of food until the next experiment one week later.

In both situations, a planarian was placed on a random spot on the filter paper and let free to move until contacting the track. The reaction of the planarian after finding the slime or soil track was recorded. A one-way analysis of variance, followed by a Tukey's test, was conducted by means of the program IBM SPSS Statistics 19 in order to determine whether the time spent by the planarians over the tracks of different prey species was significantly different.

## **Results**

### ***Prey preference***

Only the land gastropods *B. similaris*, *H. aspersa* and *D. laevis* were captured and consumed by *O. ladislavii*. There was one single attempt to capture an earthworm

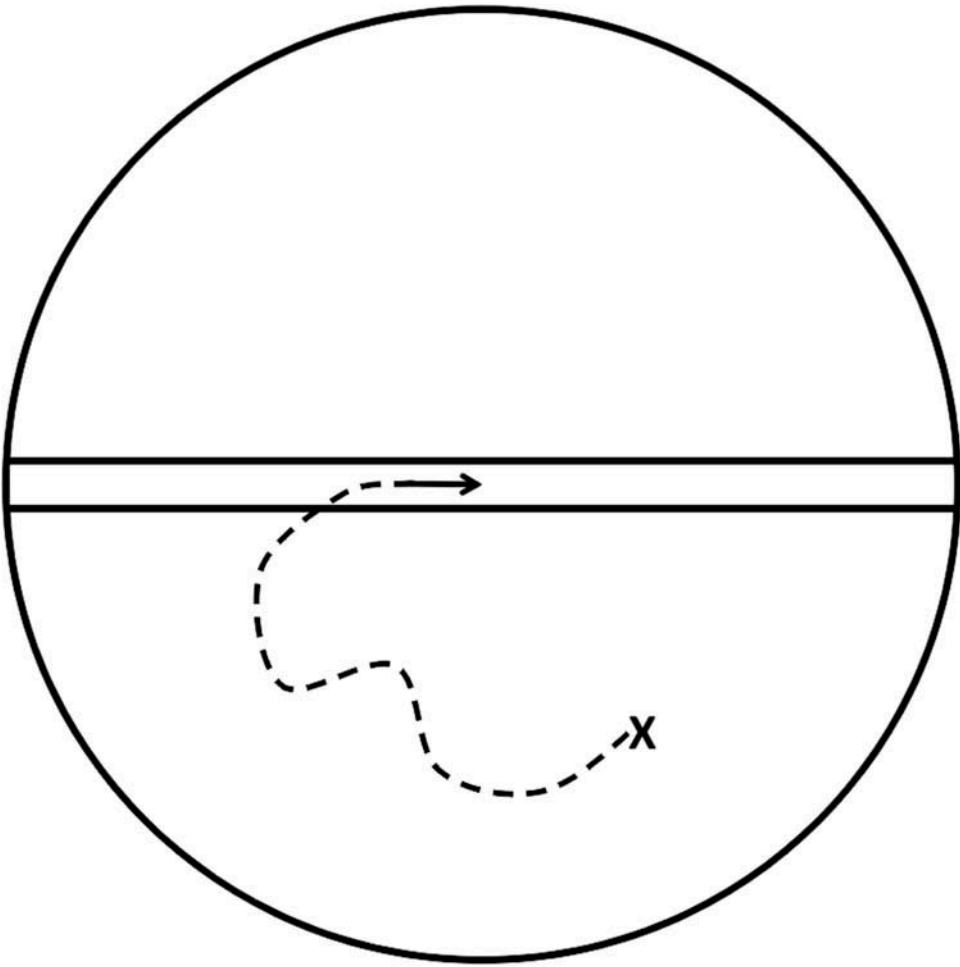


Figure 1. Experimental design for determining prey tracking behaviour. Solid line indicates outline of the slime trail. Dashed line indicates a possible path taken by the planarian, and X the planarian's initial position.

*A. gracilis* and a slug *M. pictum*. Since no other attempts were made, these two events were not included in the statistical analyses. All other invertebrates were ignored (Table 1). There was a high success rate (over 75% of attempts) for all three prey species, and there was no significant difference between them ( $\chi^2 = 1.02$ ;  $df = 2$ ;  $p = 0.6$ ).

Upon contacting the snails *B. similaris* and *H. aspersa*, *O. ladislavii* quickly slid over each shell, surrounding it, and placed its mouth close to the shell opening (Figure 2A–D). The snail did not seem to be aware of the danger until the planarian everted its pharynx, when the snail increased its speed. *Bradybaena similaris* also began to move its shell abruptly from side to side (Figure 2E–F). After some time, being unable to escape, the snail retracted into its shell (Figure 2G) and started to exude froth (Figure 3A) which, however, did not stop the attack. The planarian's

Table 1. Predation by *Obama ladislavii*, using 25 individuals, on offered invertebrate species. Asterisks indicate exotic species.

Species	Experiments	Capture		Consumption	
		Attempts N (%)	Success N (%)	Total N (%)	Partial N (%)
Gastropoda					
<i>Bradybaena similaris</i> (Férussac)*	15	13 (86.7)	12 (92.3)	11 (91.7)	1 (8.3)
<i>Helix aspersa</i> Müller*	15	14 (93.3)	11 (78.6)	5 (45.5)	6 (54.5)
<i>Meghinatium pictum</i> (Stoliczka)*	15	1 (6.7)	0 (0)	— (—)	— (—)
<i>Deroceras laeve</i> Müller*	15	14 (93.3)	12 (85.7)	12 (100)	0 (0)
<i>Happia</i> sp.	10	0 (0)	— (—)	— (—)	— (—)
Isopoda					
<i>Atlantoscia floridana</i> (Van Name)	15	0 (0)	— (—)	— (—)	— (—)
<i>Balloniscus glaber</i> Araujo & Zardo	15	0 (0)	— (—)	— (—)	— (—)
<i>Balloniscus sellowii</i> (Brandt)	15	0 (0)	— (—)	— (—)	— (—)
<i>Porcellio scaber</i> (Latreille)	15	0 (0)	— (—)	— (—)	— (—)
<i>Armadillidium</i> sp.*	10	0 (0)	— (—)	— (—)	— (—)
Isoptera					
<i>Nasutitermes</i> sp.	11	0 (0)	— (—)	— (—)	— (—)
Oligochaeta					
<i>Eisenia fetida</i> (Savigny)*	15	0 (0)	— (—)	— (—)	— (—)
<i>Amyntas gracilis</i> (Rosa)*	15	1 (6.7)	0 (0)	— (—)	— (—)
<i>Urobenus</i> sp.	10	0 (0)	— (—)	— (—)	— (—)
Tricladida					
<i>Endeavouria septemlineata</i> (Hyman)*	10	0 (0)	— (—)	— (—)	— (—)
<i>Luteostriata abundans</i> (Graff, 1899)	10	0 (0)	— (—)	— (—)	— (—)
Blattodea	10	0 (0)	— (—)	— (—)	— (—)
Collembola	15	0 (0)	— (—)	— (—)	— (—)
Diplopoda	15	0 (0)	— (—)	— (—)	— (—)
Dermaptera	11	0 (0)	— (—)	— (—)	— (—)
Elatерidae	10	0 (0)	— (—)	— (—)	— (—)

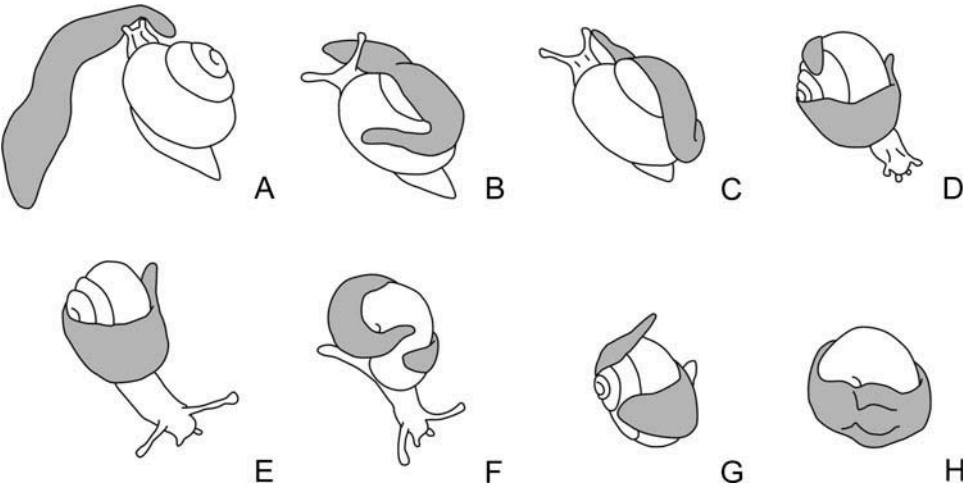


Figure 2. *Obama ladislavii* capturing *Bradybaena similaris*: (A) planarian encountering the snail; (B, C) planarian sliding over the snail's shell; (D) planarian placing the mouth close to the shell opening; (E, F) snail attempting to escape; (G) snail retracted into the shell; (H) planarian feeding on snail.

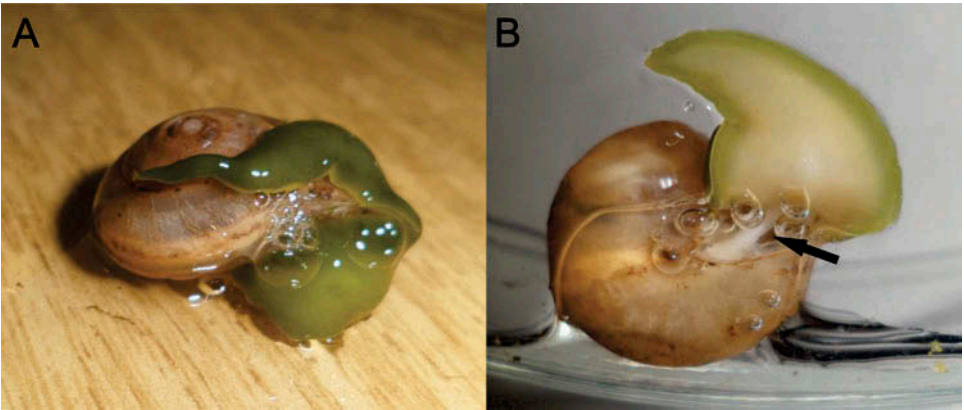


Figure 3. *Obama ladislavii* feeding on *Bradybaena similaris*: (A) planarian attached to the snail's shell and snail exuding froth after retracting into the shell; (B) planarian's everted pharynx (arrow) penetrating the snail's body.

pharynx, already everted and inserted in the snail's body, remained by the shell opening and the planarian began the process of food ingestion (Figure 2H; Figure 3B). Smaller snails were entirely ingested, with only the empty shell remaining, while larger ones were usually only partially consumed.

In order to capture *D. laevis*, *O. ladislavii* quickly attached to the slug's body with muscular movements and moved towards the slug's head to block its escape (Figure 4A–D). The slug immediately started an escape response by moving faster

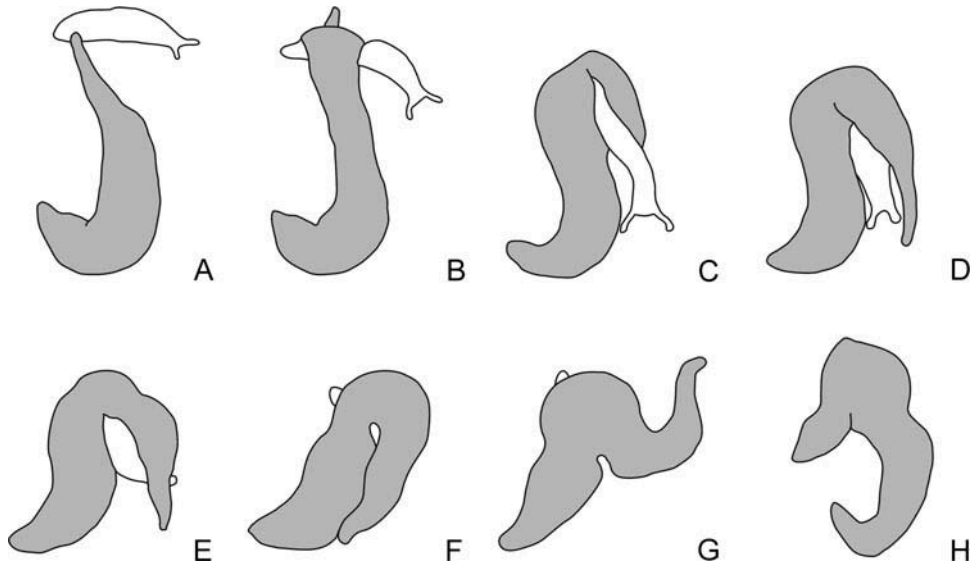


Figure 4. *Obama ladislavii* capturing *Deroceras laeve*: (A) planarian encountering the slug; (B) planarian attaching its anterior end to the slug; (C, D) planarian moving towards the slug's head to prevent escape; (E–H) slug surrounded by the planarian and pressed against the substrate.

and, in an attempt to change its direction, found itself surrounded by the planarian's body and was entirely covered by it and pressed against the substrate (Figure 4E–H). The planarian everted its pharynx and the slug was entirely ingested.

#### Prey-tracking mechanism

After contacting slime tracks left by *B. similaris*, *H. aspersa* and *D. laeve* on the filter paper, *O. ladislavii* ceased to move and attached the ventral surface of its anterior end to the track, then performed horizontal and vertical movements with the anterior end, apparently trying to locate the source of the track nearby. Unable to find the prey, it placed its anterior end over the continuation of the track and began to follow it, stopping continually during the path to repeat the movements with the anterior end. After reaching the end of the track, it returned through it from the opposite direction, until eventually resuming moving randomly over the paper. The same behaviour was not observed in the earth track, where the planarian continued to move randomly after contacting it. The mean time spent on slime tracks was significantly lower for *H. aspersa* when compared to both *B. similaris* and *D. laeve* (ANOVA.  $F = 16.198$ ;  $df = 2,15$ ;  $p < 0.001$ ) (Figure 5).

#### Discussion

Due to its common presence at human-disturbed sites, including urban areas, *O. ladislavii* faces diverse environments that are often quite different from its native ecosystem. The ability to adapt to those environments suggests a more generalist diet



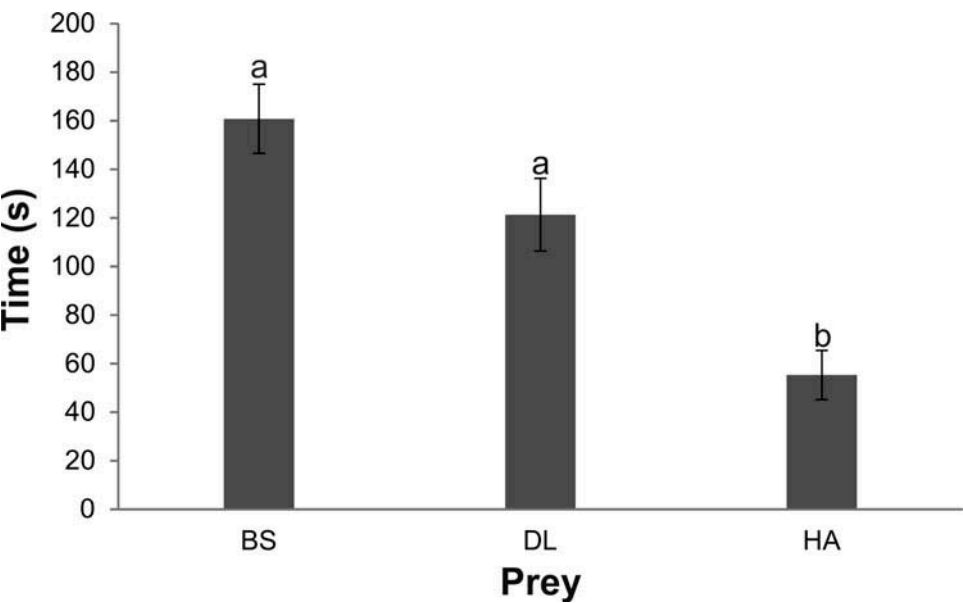


Figure 5. Mean amount of time, in seconds, spent by *Obama ladislavii* on slime of three different prey species. BS = *Bradybaena similaris* ( $160.83 \pm 35.72$ ); DL = *Deroceras laeve* ( $121.33 \pm 35.54$ ); HA = *Helix aspersa* ( $55.33 \pm 24.83$ ). Different letters indicate significant difference in means.

since the chances of finding native prey in human-disturbed areas can be low. Our results revealed the ability of *O. ladislavii* to prey on exotic gastropods that share the same habitat. Several invasive land planarians have shown the same capacity to adapt their diet to include non-native species; namely *Platydemus manokwari*, *Kontikia ventrolineata*, *Endeavouria septemlineata*, *Arthurdendyus triangulatus* and *Bipalium adventitium* (Mead 1963; Barker 1989; Blackshaw 1990; Ducey et al. 1999; Sugiura et al. 2006), all of which have become serious threats for the conservation of native ecosystems (Sugiura et al. 2006; Murchie and Gordon 2013). Among those, *P. manokwari* is usually linked to the decline of populations of land gastropods in Pacific islands (Sugiura et al. 2006). This species may be expanding its range and was recently recorded in Europe (Justine et al. 2014).

The first observations on the behaviour of land planarians indicated that food was found by accidental contacts between planarians and prey during apparently random movements through the environment (Jennings 1959). Such a blind search would be very inefficient. Although accidentally encountering prey does occur in some situations, the change in behaviour of the planarian upon reaching the slime trail allow direct location of nearby prey, and also allow detection of chemical trails left by prey, which could guide the planarian towards prey (Ogren 1956, 1995; Fiore et al. 2004; Iwai et al. 2010). The ability to detect and follow chemical trails left by the prey is demonstrated for the first time in a species of Geoplaninae. Such a behaviour was already observed in species of other subfamilies of land planarians such as Bipaliinae and Rhynchodeminae, using similar experiments (Fiore et al. 2004; Winsor et al. 2004; Iwai et al. 2010), as well as in other predators of land gastropods,



such as the predatory snail *Euglandina rosea* (Férrussac) and carabid beetles (Parakinen 1994; Holland et al. 2012; Ng et al. 2013). The presence of sensorial pits in the anterior region of the body of land planarians (Dendy 1891; Carbayo 2010) may be related to this ability to detect chemical trails. The fact that the planarian moved back and forth along the trail, similar to what has been recorded for *B. adventitium* and *P. manokwari* (Fiore et al. 2004; Iwai et al. 2010), seems to indicate an inability to detect the trail direction, but represents a strategy that greatly increases the probability of locating prey (Iwai et al. 2010). The soil track, despite its different composition in relation to the rest of the surface in the Petri dish, did not have any component signalling the presence of a prey nearby, this being the most likely explanation for the lack of interest by the planarian.

With its relatively slow movements, as compared to *L. abundans* and *B. kewense* (P. Boll, personal observation), *O. ladislavii* apparently has difficulty capturing species with rapid movements, such as arthropods or earthworms. *Luteostriata abundans* feeds on land isopods and uses quick movements of the anterior or posterior end of the body to immediately envelop the prey (Prasniski and Leal-Zanchet 2009), while *O. ladislavii* captures land gastropods by a much slower approach. However, the possible inclusion of some of the experimentally rejected organisms in the planarians' diet cannot be completely excluded because our observations were made under artificial conditions and thus some behaviours may not reflect precisely the natural responses of the planarians to their prey (Dindal 1970).

*Obama ladislavii* included exotic species of land gastropods in its diet, which indicates an ability to adapt its feeding habits to include the available species in the area. If introduced at sites outside of their original distribution, land planarians with a broad diet may become invasive and threaten local fauna (Winsor et al. 2004). The main threat is related to the slow reaction of the non-native prey, which, not having evolved in an environment with that predator, may realize the danger only when the planarian is already starting the feeding process (Fiore et al. 2004). Such slow reaction was noticed in both snail species, as the escape behaviour started after the beginning of the injuries inflicted by the planarian. On the other hand, *D. laeve* started an escape response soon after the contact with the planarian, which may be due to the fact that a fast response to tactile stimuli is important to escape the attack of its native predators, such as carabid beetles (Parakinen 1994; Jordaens et al. 2003). The different responses could also be due to the presence of an external shell in snails, which would reduce direct contact of the planarian with the snail's body.

Land gastropods constitute the known diet of several other land planarians (Froehlich 1955; Jennings 1959; Barker 1989; Winsor et al. 2004), including major invasive species (Mead 1963; Barker 1989; Kaneda et al. 1990; Ogren 1995). Thus, they comprise a group widely threatened by the invasion of exotic land planarians, and many populations of these species declined or even became extinct as a result of high predation pressure (Sugiura et al. 2006; Sugiura and Yamaura 2009; Sugiura 2010).

Alternatively, in their native areas, land planarians with a broad diet may be efficient in controlling the population of invasive species on which they are able to feed. Since *O. ladislavii* fed efficiently on very common invasive gastropods (*H. aspersa*, *B. similaris* and *D. laeve*), it has a potential use as a biological control of those species in areas where they are of environmental and economic concern. However, as in several other cases of biological pest control, the potential use of land planarians for the control of invasive species must be managed with caution to

avoid impacts on the native biota. In Hawaii, the native planarian *E. septemlineata* has been shown to be efficient in controlling populations of the giant African land snail *Achatina fulica* (Férussac), which was introduced in the archipelago. However, the abundant availability of prey led to an increase in the population of the native planarian, which in turn posed a threat to the native snails, which, due to their low population density, were not a main item of the planarian's diet (Mead 1963). Also, the higher density of planarians needed for biological control could increase accidental transport beyond its native habitat if plant products are brought into such areas.

Our results demonstrate the predation of non-native organisms by *O. ladislavii* and its ability to detect and follow chemical tracks. These characteristics, combined with its adaptability to disturbed environments, suggest that this species has the potential to become invasive if introduced to areas outside of its original range, especially south-eastern USA, Europe, south-eastern Asia, New Zealand and eastern Australia, which have climates similar to that in its native area in southern Brazil (Kottek et al. 2006). On the other hand, the flatworm has a potential to be used as a biological control in its native area for pest management at sites infested by exotic land gastropods, if further studies indicate this as a plausible action.

### Acknowledgements

We are grateful to the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and the Fundação de Amparo à Pesquisa do Rio Grande do Sul (FAPERGS) for research grants. We thank Ilana Rossi, Silvana Amaral, Giuly Iturralde, João Braccini, Ana Laura Moraes, Virginia Lemos, Lisandro Negrete and João Laux for collecting planarians and other invertebrates; Eduardo Colley for helping to identify the species of gastropods; and Emily Toriani-Moura for the English revision of the manuscript. We also thank two anonymous reviewers for their suggestions.

### References

- Antunes MB, Marques DIL, Leal-Zanchet AM. 2008. Composição de comunidades de planárias terrestres (Platyhelminthes, Tricladida, Terricola) em duas áreas de floresta estacional semidecidual do sul do Brasil. [Land flatworm (Platyhelminthes, Tricladida, Terricola) community composition in two areas of semi-deciduous forest in southern Brazil]. *Neotrop Biol Cons.* 3:34–38. Portuguese.
- Barker GM. 1989. Flatworm predation of terrestrial molluscs in New Zealand, and a brief review of previous records. *New Zeal Entomol.* 12:75–79. doi:10.1080/00779962.1989.9722571
- Blackshaw RP. 1990. Studies on *Artioposthia triangulata* (Dendy) (Tricladida: Terricola), a predator of earthworms. *Ann Appl Biol.* 116:169–176. doi:10.1111/j.1744-7348.1990.tb06596.x
- Carbayo F. 2010. A new genus for seven Brazilian land planarian species, split off from *Notogynaphallia* (Platyhelminthes, Tricladida). *Belg J Zool.* 140:91–101.
- Castro RS, Leal-Zanchet AM. 2005. Composição de comunidades de planárias terrestres (Platyhelminthes) em áreas de floresta estacional decidual e de campo na região central do Rio Grande do Sul, Brasil. [Community composition of land flatworms (Platyhelminthes) in areas of deciduous forest and grassland of the central region of Rio Grande do Sul, southern Brazil]. *Acta Biol Leopold.* 27:147–150. Portuguese.

- Cumming MS. 1995. Activity patterns of termite-eating land planarians *Microplana termitophaga* (Platyhelminthes: Tricladida). J Zool. 237:531–542. doi:[10.1111/j.1469-7998.1995.tb05013.x](https://doi.org/10.1111/j.1469-7998.1995.tb05013.x)
- Dendy A. 1891. On the presence of ciliated pits in Australian land planarians. Proc R S Victoria. 4:36–46.
- Dindal DL. 1970. Feeding behavior of a terrestrial turbellarian *Bipalium adventitium*. Am Midl Nat. 83:635–637. doi:[10.2307/2423970](https://doi.org/10.2307/2423970)
- Ducey PK, McCormick M, Davidson E. 2007. Natural history observations on *Bipalium* cf. *vagum* Jones and Sterrer (Platyhelminthes: Tricladida), a terrestrial broadhead planarian new to North America. Southeast Nat. 6:449–460. doi:[10.1656/1528-7092\(2007\)6\[449:NHOBC\]2.0.CO;2](https://doi.org/10.1656/1528-7092(2007)6[449:NHOBC]2.0.CO;2)
- Ducey PK, Messere M, Lapoint K, Noce S. 1999. Lumbricid prey and potential herpetofaunal predators of the invading terrestrial flatworm *Bipalium adventitium* (Turbellaria: Tricladida: Terricola). Am Midl Nat. 141:305–314. doi:[10.1674/0003-0031\(1999\)141\[0305:LPAPHP\]2.0.CO;2](https://doi.org/10.1674/0003-0031(1999)141[0305:LPAPHP]2.0.CO;2)
- Fick IA, Leal-Zanchet AM, Vieira EM. 2006. Community structure of land flatworms (Platyhelminthes, Terricola): comparisons between Araucaria and Atlantic Forest in Southern Brazil. Invertebr Biol. 125:306–313. doi:[10.1111/j.1744-7410.2006.00062.x](https://doi.org/10.1111/j.1744-7410.2006.00062.x)
- Fiore C, Tull JL, Zehner S, Ducey PK. 2004. Tracking and predation on earthworms by the invasive terrestrial planarian *Bipalium adventitium* (Tricladida, Platyhelminthes). Behav Process. 67:327–334. doi:[10.1016/j.beproc.2004.06.001](https://doi.org/10.1016/j.beproc.2004.06.001)
- Froehlich CG. 1955. On the biology of land planarians. Bol Fac Fil Ci Letr Zoologia. 20:263–271.
- Froehlich CG. 1959. On geoplanids from Brazil. Bol Fac Fil Ci Letr Zoologia. 22:201–265.
- Holland BS, Chock T, Lee A, Sugiura S. 2012. Tracking behavior in the snail *Euglandina rosea*: first evidence of preference for endemic vs. biocontrol target pest species in Hawaii. Am Malac Bull. 30:153–157. doi:[10.4003/006.030.0113](https://doi.org/10.4003/006.030.0113)
- Iwai N, Sugiura S, Chiba S. 2010. Prey-tracking behavior in the invasive terrestrial planarian *Platydemus manokwari* (Platyhelminthes, Tricladida). Naturwissenschaften. 97:997–1002. doi:[10.1007/s00114-010-0717-4](https://doi.org/10.1007/s00114-010-0717-4)
- Jennings JB. 1959. Observations on the nutrition of the land planarian *Orthodemus terrestris*. Biol Bull. 117:119–124. doi:[10.2307/1539043](https://doi.org/10.2307/1539043)
- Jordaens K, Gielen H, Van Houtte N, Bernon G, Beckeljaun T. 2003. The response of the terrestrial slug *Deroceras laeve* to the mucus and air-borne odours of con- and hetero-specifics (Pulmonata: Agriolimacidae). J Moll Stud. 69:285–288. doi:[10.1093/mollus/69.3.285](https://doi.org/10.1093/mollus/69.3.285)
- Justine JL, Winsor L, Gey D, Gros P, Thévenot J. 2014. The invasive New Guinea flatworm *Platydemus manokwari* in France, the first record for Europe: time for action is now. PeerJ. 2:e297.
- Kaneda M, Kitagawa K, Ichinohe F. 1990. Laboratory rearing methods and biology of *Platydemus manokwari* De Beauchamp (Tricladida: Terricola: Rhynchodemidae). Appl Entomol Zool. 25:524–528.
- Kottek M, Grieser J, Beck C, Rudolf B, Rubel F. 2006. World map of the Köppen-Geiger climate classification updated. Meteorol Z. 15:259–263. doi:[10.1127/0941-2948/2006/0130](https://doi.org/10.1127/0941-2948/2006/0130)
- Leal-Zanchet AM, Baptista VA, Campos LM, Raffo JF. 2011. Spatial and temporal patterns of land flatworm assemblages in Brazilian Araucaria forests. Invertebr Biol. 130:25–33. doi:[10.1111/j.1744-7410.2010.00215.x](https://doi.org/10.1111/j.1744-7410.2010.00215.x)
- Lemos VS, Canello R, Leal-Zanchet AM. 2012. Carnivore mollusks as natural enemies of invasive land flatworms. Ann Appl Biol. 161:127–131. doi:[10.1111/j.1744-7348.2012.00556.x](https://doi.org/10.1111/j.1744-7348.2012.00556.x)
- Graff L. 1899. Monographie der Turbellarien. II. Tricladida Terricola. [Monography of the turbellarians. II. Tricladida Terricola]. Leipzig: Engelmann.

- McDonald JC, Jones HD. 2014. Feeding, maintenance and reproduction of *Microplana terrestris* (Platyhelminthes: Tricladida: Continenticola: Geoplaninae: Microplaninae) under laboratory conditions. *J Nat Hist.* 48:1–34. doi:[10.1080/00222933.2013.809169](https://doi.org/10.1080/00222933.2013.809169)
- Mead AR. 1963. A flatworm predator of the giant African snail *Achatina fulica* in Hawaii. *Malacologia.* 1:305–309.
- Murchie AK, Gordon AW. 2013. The impact of the ‘New Zealand flatworm’, *Arthurdendyus triangulatus*, on earthworm populations in the field. *Biol Invasions.* 15:569–586. doi:[10.1007/s10530-012-0309-7](https://doi.org/10.1007/s10530-012-0309-7)
- Murchie AK, Moore JP, Walters KFA, Blackshaw RP. 2003. Invasion of agricultural land by the earthworm predator, *Arthurdendyus triangulatus* (Dendy). *Pedobiologia.* 47:920–923.
- Ng TPT, Saltin SH, Davies MS, Johannesson K, Stafford R, Williams GA. 2013. Snails and their trails: the multiple functions of trail-following in gastropods. *Biol Rev.* 88:683–700. doi:[10.1111/brv.12023](https://doi.org/10.1111/brv.12023)
- Ogren RE. 1956. Physiological observations on movement and behavior of the land planarian *Rhynchodemus sylvaticus* (Leidy). *Proc Pa Acad Sci.* 30:218–225.
- Ogren RE. 1995. Predation behaviour of land planarians. *Hydrobiologia.* 305:105–111. doi:[10.1007/BF00036370](https://doi.org/10.1007/BF00036370)
- Parakinen E. 1994. The importance of mucus as a defence against carabid beetles by the slugs *Arion fasciatus* and *Deroceras reticulatum*. *J Moll Stud.* 69:285–288.
- Peel MC, Finlayson BL, McMahon TA. 2007. Updated world map of the Köppen-Geiger climate classification. *Hydrol Earth Syst Sci.* 11:1633–1644. doi:[10.5194/hess-11-1633-2007](https://doi.org/10.5194/hess-11-1633-2007)
- Prasniski MET, Leal-Zanchet AM. 2009. Predatory behavior of the land flatworm *Notogynaphallia abundans* (Platyhelminthes: Tricladida). *Zoologia.* 26:606–612. doi:[10.1590/S1984-46702009005000011](https://doi.org/10.1590/S1984-46702009005000011)
- Sluys R. 1998. Land planarians (Platyhelminthes, Tricladida, Terricola) in biodiversity and conservation studies. *Pedobiologia.* 42:490–494.
- Sugiura S. 2010. Prey preference and gregarious attacks by the invasive flatworm *Platydemus manokwari*. *Biol Invasions.* 12:1499–1507. doi:[10.1007/s10530-009-9562-9](https://doi.org/10.1007/s10530-009-9562-9)
- Sugiura S, Okochi I, Tamada H. 2006. High predation pressure by an introduced flatworm on land snails on the oceanic Ogasawara Islands. *Biotropica.* 38:700–703. doi:[10.1111/j.1744-7429.2006.00196.x](https://doi.org/10.1111/j.1744-7429.2006.00196.x)
- Sugiura S, Yamaura Y. 2009. Potential impacts of the invasive flatworm *Platydemus manokwari* on arboreal snails. *Biol Invasions.* 11:737–742. doi:[10.1007/s10530-008-9287-1](https://doi.org/10.1007/s10530-008-9287-1)
- Winsor L. 1983. A revision of the cosmopolitan land planarian *Bipalium kewense* Moseley, 1878 (Turbellaria: Tricladida: Terricola). *Zool J Linn Soc Lond.* 79:61–100. doi:[10.1111/j.1096-3642.1983.tb01161.x](https://doi.org/10.1111/j.1096-3642.1983.tb01161.x)
- Winsor L, Johns PM, Barker GM. 2004. Terrestrial planarians (Platyhelminthes: Tricladida: Terricola) predaceous on terrestrial gastropods. In: Barker GM, editor. *Natural enemies of terrestrial molluscs*. Wallingford, CT: CAB International; p. 227–278.
- Zaborski ER. 2002. Observations on feeding behavior by the terrestrial flatworm *Bipalium adventitium* (Platyhelminthes: Tricladida: Terricola) from Illinois. *Am Midl Nat.* 148:401–408. doi:[10.1674/0003-0031\(2002\)148\[0401:OOFBBT\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2002)148[0401:OOFBBT]2.0.CO;2)