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Diversity out of simplicity: interaction behavior of land planarians with co-occurring invertebrates

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ABSTRACT

Land planarians have a simple anatomy and simple behavioral repertoire in relation to most bilaterian animals, which makes them adequate for the study of biological processes. In this study, we investigate the behavior of land planarians during interaction events with other invertebrates found in the same environment. We observed 16 different behavioral units, including seven different capture behaviors and three different prey ingestion behaviors. The capture behavior varied from very simple, such as simply covering the prey with the body, to more complex ones, including two forms of tube formation that are described for the first time. In general, the capture behaviors were similar among different predators but different for different prey. Similarly, prey ingestion type was more related to prey type than to predator species, with small soft prey being swallowed without fragmentation, large prey being crushed, and prey with a hard skeleton being perforated. Considering that land planarians face limitations due to their lack of efficient ways to retain water, thus being highly dependent on a moist environment, the set of behaviors shown by them in this study was considerably rich, especially concerning strategies to capture prey.

1. Introduction

In animals with simple anatomy and without social organization, behavioral strategies to obtain food and avoid predation are usually the most diversified and are strongly related to the organism's evolutionary history and anatomy, as well as to the ecological context in which it is found (Alcock, 2001; Whelan and Schmidt, 2007). Flatworms are considered simple animals and, just like their anatomy, their behavior is much simpler than that of other animals, such as mollusks, arthropods and vertebrates (Corning and Kelly, 1973; Sheiman and Tiras, 1996).

Various comments on the behavior and diet of land planarians as observed during collection and maintenance are presented in many publications focused on the description of new species since the group was discovered (Darwin, 1844; Moseley, 1877; Goetsch, 1933). Among the works on the behavior of land planarians, most are observations on their behavior in face of different stimuli (Lehnert, 1891; Kawaguti, 1932; Ogren, 1956) or, when directed to their predatory behavior, are focused on species that are invasive in the Northern hemisphere due to the threat they may present to ecosystems (Dindal, 1970; Zaborski, 2002; Fiore et al., 2004; Ducey et al., 2007; Sugiura, 2010).

Concerning the Neotropical region, Froehlich (1955) briefly described the predatory behavior of several native planarians. Later studies gathered more detailed information on the predatory behavior of six native species (Hauser and Maurmann, 1959; Prasniski and Leal-Zanchet, 2009; Boll and Leal-Zanchet, 2015, 2016; Cseh et al., 2017) and one exotic species (Boll et al., 2015) common to human-disturbed areas. These works showed that these species feed on different invertebrates and presented data regarding the strategies used by those planarians to capture prey.

In order to increase the knowledge on predatory behaviors presented by land planarians and how they relate to co-occurring invertebrate species, we investigated the behavior of six species of Neotropical land planarians that have different diets during interaction events with other invertebrates found in the same environment. We aimed to verify whether the behaviors presented by these planarians are similar for different prey consumed by the same predator or similar for the same prey consumed by different predators.

2. Materials and methods

2.1. Capture and maintenance

We captured specimens of land planarians in the field in human-disturbed areas (HDA), as well as in different forest formations

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Fig. 1. The six land planarian species used in the experiments: (a) *Obama anthropophila*; (b) *Obama ficki*; (c) *Obama ladislavii*; (d) *Obama nungara*; (e) *Paraba multicolor*; (f) *Luteostriata abundans*. Anterior end of the planarians to the left. Scale bars = 10 mm.

belonging to the Atlantic Forest biome, viz. Araucaria Moist Forest (AMF), Subtropical Atlantic Forest (SAF), Deciduous Seasonal Forest (DSF) and Semi-Deciduous Seasonal Forest (SSF).

We selected the following six species (with their respective number of individuals (*N*) and areas of capture) according to their availability (Fig. 1): *Luteostriata abundans* (Graff, 1899) (*N* = 30; HDA, DSF, SSF); *Obama anthropophila* Amaral, Leal-Zanchet & Carbayo, 2015 (*N* = 41; HDA, AMF, DSF, SSF); *Obama ficki* (Amaral and Leal-Zanchet, 2012) (*N* = 12; SSF, DSF, AMF, SAF); *Obama ladislavii* (Graff, 1899) (*N* = 27; HDA, AMF, SAF, DSF); *Obama nungara* Carbayo, Álvarez-Presas, Jones & Riutort, 2016 (*N* = 10; HDA); and *Paraba multicolor* (Graff, 1899) (*N* = 20; HDA).

In the same localities, we captured other invertebrates in order to observe how the planarians interact with them (asterisks indicate exotic species): land gastropods – snails *Bradybaena similaris* (Férussac, 1821)* and *Helix aspersa* (O.F. Müller, 1774)*; slugs *Deroceras laeve* (O.F. Müller, 1774)*, *Meghimatium pictum* (Stolitzka, 1873)*, *Sarasinula plebeia* (P. Fischer, 1868) and *Belocaulus* sp.); earthworms *Eisenia andrei* Bouché, 1972*, *Metaphire schmardae* (Horst, 1883)* and *Amynthas gracilis* (Kinberg, 1867)*; land planarians – *Endeavouria septemlineata* (Hyman, 1939)* and *Dolichoplana carvalhoi* Corrêa, 1947*; woodlice – *Atlantoscia floridana* (van Name, 1940), *Balloniscus glaber* Araujo & Zardo, 1995, *Benthana cairensis* Skolowicz, Araujo & Boelter, 2008, *Porcellio scaber* Latreille, 1804* and *Armadillidium vulgare* Latreille, 1804*; harvestmen –*Discocyrtus* cf. *dilatatus* Sørensen, 1884, Gonyleptidae 1 and Gonyleptidae 2; termites – *Nasutitermes* sp., ants – *Camponotus* sp. and *Solenopsis* sp.; millipedes – *Rhinocricus* sp. 1, *Rhinocricus* sp. 2. and *Obiricodesmus* sp.; and unidentified species of Hirudinea, Entomobryidae, Hypogastruridae, Blattodea, Dermaptera and larvae of Elateridae, Passalidae and Mycetophilidae.

In the laboratory, we maintained the specimens in small plastic terraria containing moist soil, leaves, and log fragments to simulate their natural environment. The terraria remained in the dark at a temperature ranging between 18 °C and 20 °C and a relative air humidity of about 90%.

We also tested the interaction of the four planarians of the genus *Obama* with each other and of *Luteostriata abundans* with the other five species. Interactions of *Paraba multicolor* with species of *Obama* were not included in the study because not enough specimens of *P. multicolor* were simultaneously available in the laboratory.

We made the observations reported herein simultaneously with the experiments reported in Boll and Leal-Zanchet (2016), where we presented the results related to the diet identified for each species.

2.2. Investigation of interactive behaviors

To record the behavior of the planarians when interacting with other invertebrates, we put one land planarian in a moistened Petri dish together with a specimen of another invertebrate species. We performed 15 repetitions with each invertebrate species for each planarian species, in random sequence, with intervals of three or four days between the experiments.

After recording the planarian's movements and postures in an empirical manner, we characterized the behavior in a functional manner

Table 1
Behavior units registered during the observation of six species of land planarians interacting with other invertebrates. Oban = *Obama anthropophila*, Obfi = *Obama ficki*, Obla = *Obama ladislavii*, Obnu = *Obama nungara*, Pamu = *Paraba multicolor*, Luab = *Luteostriata abundans*.

Behavioral Unit	Description	Oban	Obfi	Obla	Obnu	Pamu	Luab
Exploratory behavior (EX)	Gliding forward, touching the substrate with the anterior end	X	X	X	X	X	X
Investigative behavior (IN)	Following a cue left on the substrate	X		X			
Approaching behavior (AP)	Constant touches on the invertebrate with the anterior end	X	X	X	X	X	X
Surrounding immobilization (SU)	Surrounding the prey and pressing it against the substrate	X	X	X	X	X	
Shell climbing (SC)	Crawling onto the snail shell			X			
Covering immobilization (CO)	Covering the prey with the body	X	X	X	X	X	
Helicoidal tube formation (HT)	Forming a tube around the prey by twisting the body as a helix		X			X	
Straight tube formation (ST)	Forming a tube around the prey by bending the sides toward the venter	X			X		
Pressure immobilization (PR)	Moving over the prey and pressing it against the substrate				X		
Entrapping immobilization (EN)	Quick movements of the anterior or posterior end toward the prey						X
Pharynx positioning (PH)	Placing the mouth over the prey and everting the pharynx	X	X	X	X	X	X
Prey swallowing (PS)	Prey is sucked into the intestine without previous fragmentation	X	X	X	X	X	
Prey crushing (PC)	Pharynx is attached onto the prey's surface and tears it into smaller pieces	X	X	X	X	X	
Prey perforation (PP)	Pharynx is pierced through the prey's surface and the inner contents are sucked			X			X
Aversive behavior (AV)	Withdrawing quickly	X	X	X	X	X	X
Escape behavior (ES)	Changing direction and moving quickly away from the invertebrate						X

and in analogy to the behavior of other species (Lorenz, 1974). After this characterization, we defined and described the behavior units observed during the interactions. We also recorded the rate of occurrence of each behavior during the interaction with each invertebrate in order to identify the most frequent response of the planarians when facing each invertebrate.

3. Results

The observations of the interaction of land planarians with other invertebrates led us to identify 16 different behavioral categories (Table 1) described below.

3.1. Exploratory behavior (EX)

The planarian glides slowly forward in an apparently random fashion, without noticeable muscle contractions along the body, and keeps the anterior end raised, moving it horizontally and vertically and slightly touching the surrounding substrate.

3.2. Investigative behavior (IN)

The planarian finds a cue indicating the presence of a prey nearby and follows it. This behavior was only observed in *O. anthropophila* and *O. ladislavii*. After finding a slime trail left by a potential prey (both planarians and gastropods for *O. anthropophila* and only gastropods for *O. ladislavii*), the planarian strongly attaches the ventral surface of its anterior end to the trail and starts to follow it, increasing the speed and intensity of the movements observed in the exploratory behavior.

3.3. Approaching behavior (AP)

After finding an invertebrate, the planarian constantly touches the surface of the invertebrate using the anterior end. If the invertebrate starts to move, the planarian follows it quickly, usually attaching its anterior end to it. This behavior was similar in all species.

3.4. Capture behaviors (CA)

The planarian performs muscular movements to immobilize the invertebrate. This behavior was different for different invertebrate groups and included the following six behavioral units:

(i) Surrounding immobilization (SU). After identifying a gastropod (usually a snail or large slug) as food, the planarian quickly surrounds the gastropod's head to block its escape (Figs. 2a and b, 3a–c, 4a and b), then surrounds it entirely and presses it against the substrate to immobilize it (Figs. 2c and d, 3c and d, 4c and d). With slugs, the whole body is surrounded during immobilization (Fig. 2d), while snails are usually immobilized through their exposed soft parts (Figs. 3d and e 4d). The gastropod may free itself during the attack (Fig. 3f), which induces the planarian to restart the process (Fig. 3f and g). Snails may also escape by retracting into the shell.

(ii) Shell climbing (SC). The species *O. ladislavii*, when attacking snails, usually crawls onto the shell before starting the feeding process (Fig. 5a). Thus, if the snail tries to escape, the planarian is pulled along with it (Fig. 5b; and see Boll and Leal-Zanchet, 2015). Using this approach, the planarian is able to place its pharynx close to the shell opening without the need to immobilize the prey (Fig. 5c) and usually surrounds the prey after weakening it (Fig. 5d). This behavior was not observed in any other species that consume gastropods.

(iii) Covering immobilization (CO). When finding a slug or a planarian that is much smaller than itself, the planarian may simply cover the prey with its body (Figs. 6 and 7).

(iv) Tube formation (T). The planarian grabs the prey with the anterior end (Figs. 8a 9a–c, 10a and b) and conducts it to the pharynx through a tube formed with the body. To build the tube, the planarian may twist itself as a helix around the prey (helicoidal tube (HT); Fig. 8b–d) or bend the sides of the body towards the venter (straight tube (ST); Figs. 9d–e and 10c–e). This behavior was usually applied to capture land planarians and small slugs.

(v) Pressure immobilization (PR). After contacting an earthworm, the planarian attaches its anterior end to the prey and then moves over it while pressing it against the substrate to immobilize it (Fig. 11). *O. nungara* was the only species to show this behavior.

(vi) Entrapping immobilization (EN). The contact of a woodlouse with any part of the planarian's body was instantly followed by very quick movements of the anterior or posterior end of the planarian toward the prey, wrapping it and pressing it against the substrate (Fig. 12a–c; and see Prasniski and Leal-Zanchet, 2009).

3.5. Pharynx positioning (PH)

After successfully immobilizing the prey, the planarian moved itself to place its mouth over the prey and then everted its pharynx (Figs. 2d, 3h, 4f, 11c, 12d).

Prey ingestion (PI). Once the pharynx was everted, the planarian started to ingest the prey. Prey ingestion varied according to prey type and size and included three variations:

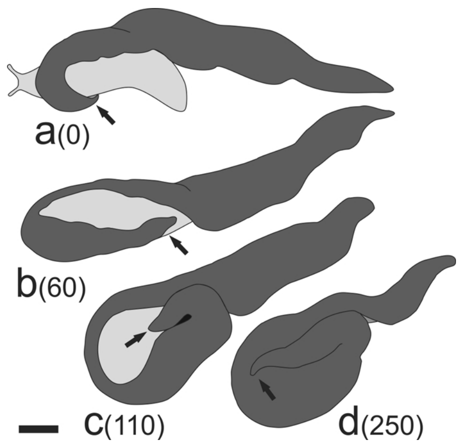

Fig. 2. *Obama ficki* capturing the slug *Meghimatium pictum*: (a) approaching behavior; (b–d) surrounding immobilization. Arrows indicate anterior end of the planarian. Scale bar = 10 mm. Numbers in parentheses indicate time in seconds from the beginning of the recorded behavior.

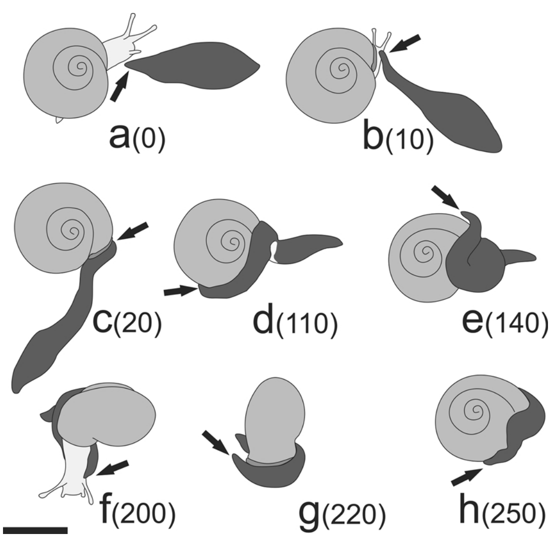

Fig. 3. *Obama anthropophila* capturing the snail *Bradybaena similaris*: (a–b) approaching behavior; (c–e) surrounding immobilization; (f–g) partial release of the snail followed by new immobilization; (h) pharynx positioning. Arrows indicate anterior end of the planarian. Scale bar = 10 mm. Numbers in parentheses indicate time in seconds from the beginning of the recorded behavior.

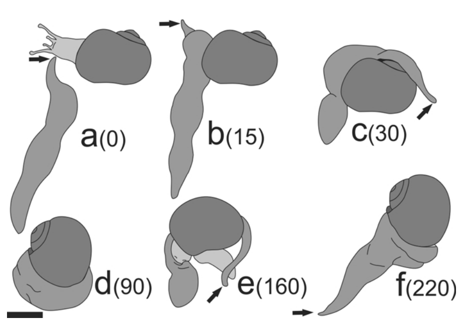

Fig. 4. *Obama ladislavii* capturing the snail *Helix aspersa*: (a) approaching behavior; (b–d) surrounding immobilization; (e–f) pharynx positioning. Arrows indicate anterior end of the planarian. Scale bar = 10 mm. Numbers in parentheses indicate time in seconds from the beginning of the recorded behavior.

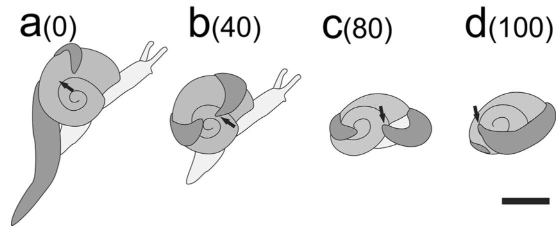

Fig. 5. *Obama ladislavii* capturing the snail *Bradybaena similaris*: (a–b) shell climbing; (c–d) pharynx positioning. Arrows indicate anterior end of the planarian. Scale bar = 10 mm. Numbers in parentheses indicate time in seconds from the beginning of the recorded behavior.

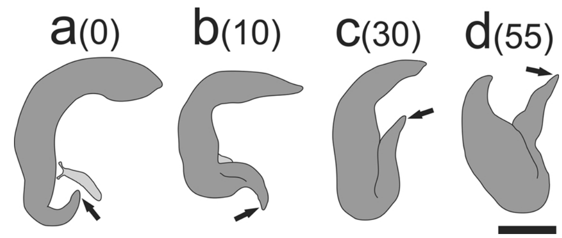

Fig. 6. *Obama ladislavii* capturing the slug *Belocaulus* sp.: (a) approaching behavior; (b–d) covering immobilization. Arrows indicate anterior end of the planarian. Scale bar = 10 mm. Numbers in parentheses indicate time in seconds from the beginning of the recorded behavior.

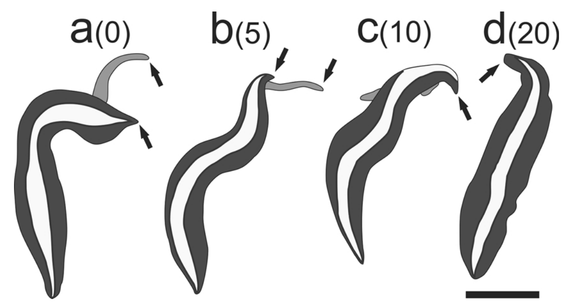

Fig. 7. *Paraba multicolor* capturing the land planarian *Endeavouria septemlineata* by covering immobilization. Arrows indicate anterior end of both planarians. Scale bar = 10 mm. Numbers in parentheses indicate time in seconds from the beginning of the recorded behavior.

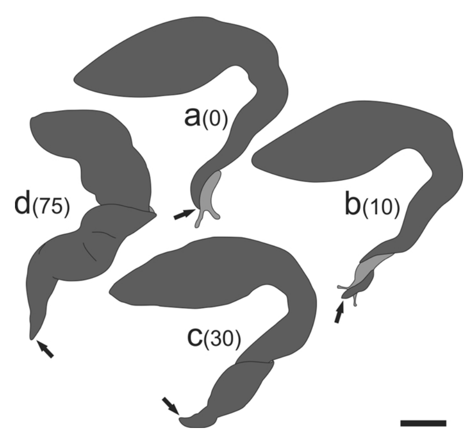

Fig. 8. *Obama ficki* capturing the slug *Deroceras leave*: (a) approaching behavior; (b–d) helicoidal tube formation. Arrows indicate anterior end of the planarian. Scale bar = 10 mm. Numbers in parentheses indicate time in seconds from the beginning of the recorded behavior.

(i) Prey swallowing (PS). The prey is sucked through the pharynx into the intestine without fragmentation or noticeable external digestion (Fig. 13). This ingestion type was used with planarians, small slugs, and small earthworms.

(ii) Prey crushing (PC). The pharynx is attached on the prey's surface and crushes it, turning the prey into smaller fragments that can be sucked into the intestine (Fig. 14). This was used to ingest snails, large

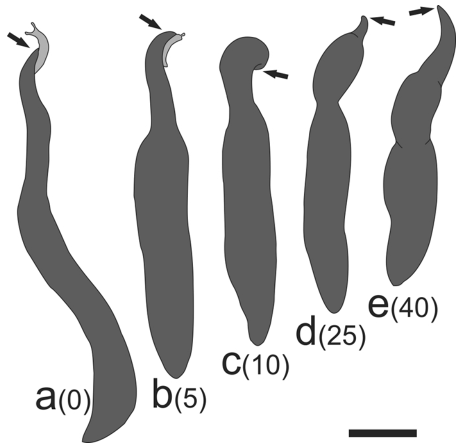

Fig. 9. *Obama anthropophila* capturing the slug *Belocaulus* sp.: (a) approaching behavior; (b–e) straight tube formation. Arrows indicate anterior end of the planarian. Scale bar = 10 mm. Numbers in parentheses indicate time in seconds from the beginning of the recorded behavior.

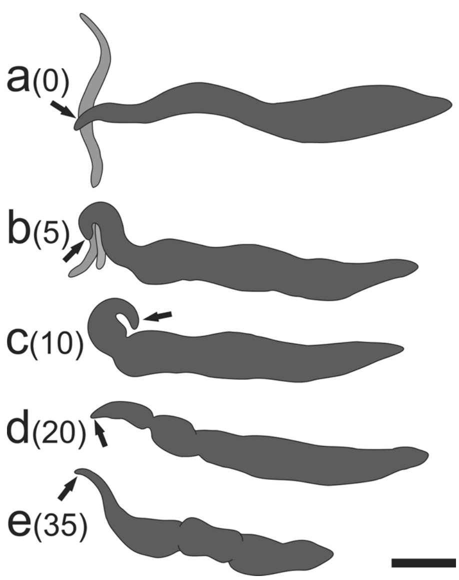

Fig. 10. *Obama anthropophila* capturing the land planarian *Endeavouria septemlineata*: (a) approaching behavior; (b–e) straight tube formation. Arrows indicate anterior end of the predatory planarian. Scale bar = 10 mm. Numbers in parentheses indicate time in seconds from the beginning of the recorded behavior.

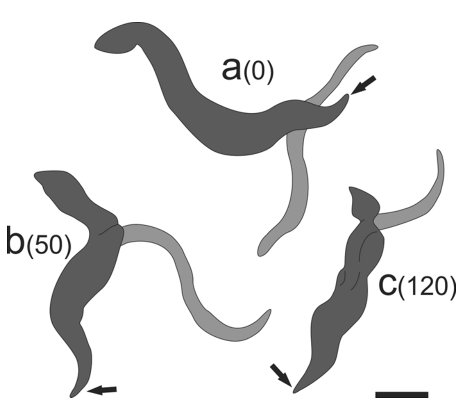

Fig. 11. *Obama nungara* capturing the earthworm *Eisenia andrei* by pressure immobilization (a–c). Arrows indicate anterior end of the planarian. Scale bar = 10 mm. Numbers in parentheses indicate time in seconds from the beginning of the recorded behavior.

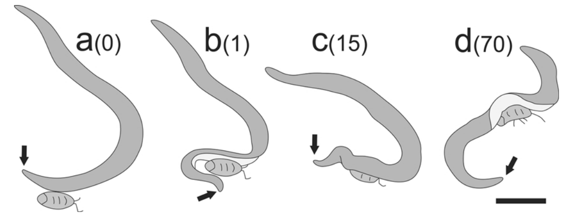

Fig. 12. *Luteostriata abundans* capturing the woodlouse *Atlantoscia floridana*: (a–c) entrapping immobilization; (d) pharynx positioning. Scale bar = 10 mm. Numbers in parentheses indicate time in seconds from the beginning of the recorded behavior.

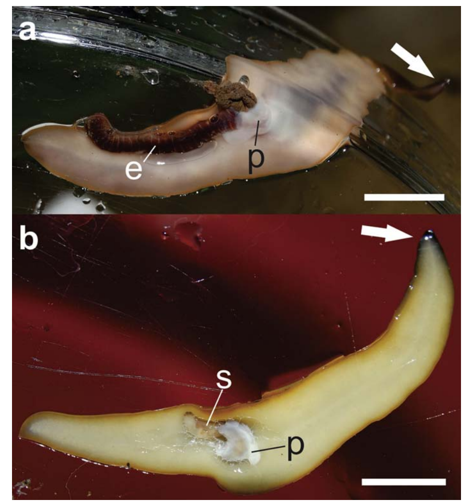

Fig. 13. Ventral view of *Obama nungara* performing prey ingestion by prey swallowing: (a) swallowing the earthworm *Eisenia andrei*; (b) swallowing the slug *Belocaulus* sp. Abbreviations: e = earthworm, p = planarian's pharynx, s = slug. Arrows indicate anterior end of the planarian. Scale bars = 10 mm.

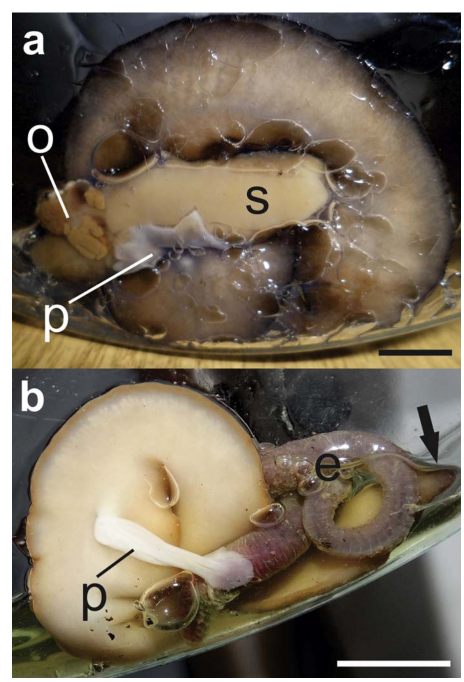

Fig. 14. Ventral view of land planarians performing prey ingestion by prey crushing: (a) *Obama ficki* feeding on the slug *Sarasinula plebeia*; (b) *Obama nungara* feeding on the earthworm *Eisenia andrei*. Abbreviations: e = earthworm, o = exposed internal organs of the slug; p = planarian's pharynx; s = slug. Arrow indicates anterior end of the planarian. Scale bars = 10 mm.

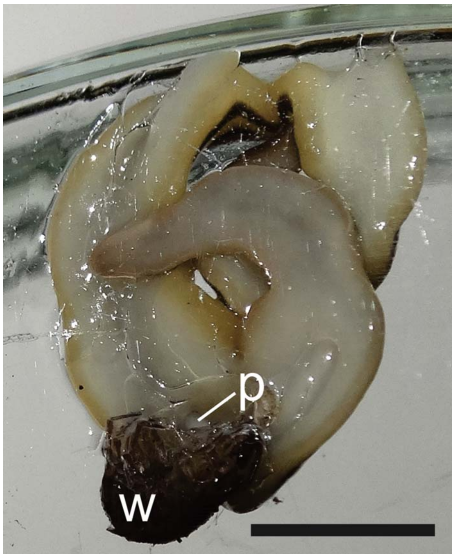

Fig. 15. Ventral view of *Luteostriata abundans* performing prey ingestion of the woodlouse *Atlantoscia floridana* by prey perforation. Abbreviations: p = planarian's pharynx; w = woodlouse. Scale bar = 10 mm.

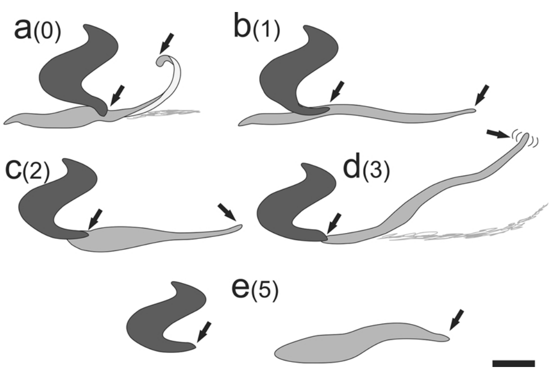

Fig. 16. Escape behavior of *Luteostriata abundans* (light gray) after interacting with *Obama anthropophila* (dark gray): (a–b) approaching behavior of *O. anthropophila* in conjunction with escape behavior of *L. abundans* by lifting the anterior half of the body and stretching it forward; (c) body contraction pulling the posterior half forward; (d) anterior half lifted a second time in conjunction with vibrations of the anterior end; (e) second body contraction releasing *L. abundans* from its predator. Arrows indicate anterior end of both planarians. Scale bar = 10 mm. Numbers in parentheses indicate time in seconds from the beginning of the recorded behavior.

slugs, and large earthworms.

(iii) Prey perforation (PP). The pharynx is pierced through the prey's surface (Fig. 15) and the prey's inner contents are ingested, usually leaving an empty shell at the end. *Luteostriata abundans* used this behavior to feed on woodlice, and *O. ladislavii* to feed on snails.

3.6. Aversive behavior (AV)

This behavior contrasted with the approaching behavior. After contacting the invertebrate with the anterior end, the planarian withdrew quickly using muscle contractions, interrupting the contact.

3.7. Escape behavior (ES)

An intense aversive behavior followed by the planarian changing direction (if facing the invertebrate) and moving quickly away from the invertebrate (Fig. 16). It was only observed in *L. abundans*. In such a response, the anterior half of the body is elongated (Fig. 16a–c) and kept raised for some seconds, usually vibrating vertically or horizontally (Fig. 16d). After touching the substrate again, the anterior end does so more distantly than in normal displacement and the body is then contracted, pulling the posterior half forward (Fig. 16e).

3.8. Overview

An ethogram was drawn to show the behavioral sequences observed during the experiments (Fig. 17). Most invertebrate species did not elicit any change in the exploratory behavior of the planarians. A capture behavior was elicited during most encounters with species identified as prey, while an escape behavior occurred after finding a species identified as a predator (Fig. 18). Approaching and aversive behaviors not followed by capture and escape behaviors did happen sometimes, but not to a great extent. *Luteostriata abundans* had the greatest number of aversive responses when interacting with several different invertebrates (Fig. 18).

Paraba multicolor and the four species of *Obama* captured gastropods. The capture behaviors were similar for different predators but different for different prey. Only *O. ladislavii* showed an exclusive behavior, SC, in the capture of snails. The behaviors used by *O. anthropophila*, *O. nungara* and *P. multicolor* to capture other land planarians were similar to the ones used to capture small slugs (Table 2).

Similarly, prey ingestion type was more related to prey type than to the predator species. Whenever possible, the planarians ingested the prey as a whole piece by sucking it into the intestine. Large prey or prey with a hard exoskeleton had to be fragmented before ingestion.

4. Discussion

Despite their simple anatomy, the land planarians in this study showed a considerably rich set of behaviors related to the interaction with other species, especially prey species. We observed 16 different behavioral units, seven of which were different capture behaviors. Additionally, we observed three different prey ingestion behaviors depending on prey type and size. The capture behavior varied from very simple, such as simply covering the prey with the body, to more complex, including two forms of tube formation that are here described for the first time.

The most basic behavior was the exploratory behavior, which is similar in all studied species. It has already been observed by previous researchers in species from different subfamilies (Darwin, 1844; Moseley, 1874; Goetsch, 1933; Froehlich, 1955; Ogren, 1956; Barker, 1989).

Only two species, *O. anthropophila* and *O. ladislavii*, were observed to follow a chemical trail left by a gastropod or planarian prey (investigative behavior). The same behavior was previously reported in *Bipalium adventitium* and *Platydemus manokwari*, two important invasive land planarians (Fiore et al., 2004; Iwai et al., 2010). Studies with other invertebrate groups, such as snails (Shearer and Atkinson, 2001), have shown that strategies used for finding food may vary between species having different diets, and the same may apply to land planarians.

As observed in the present study, the anterior region of land planarians has a fundamental role in the detection and acquisition of food, having sense organs such as ciliated pits that are likely responsible for chemoreception (Curtis et al., 1983) and a strong musculature that may assist in the capture of prey. Of the species studied herein, *L. abundans* is known to have a retractor muscle in the cephalic region (Carbayo, 2010), but it does not seem to be necessary for the capture behavior since the posterior end may be used to capture prey as well (Prasniski and Leal-Zanchet, 2009). The other studied species lack cephalic specializations but, as seen here, it does not prevent them from using their

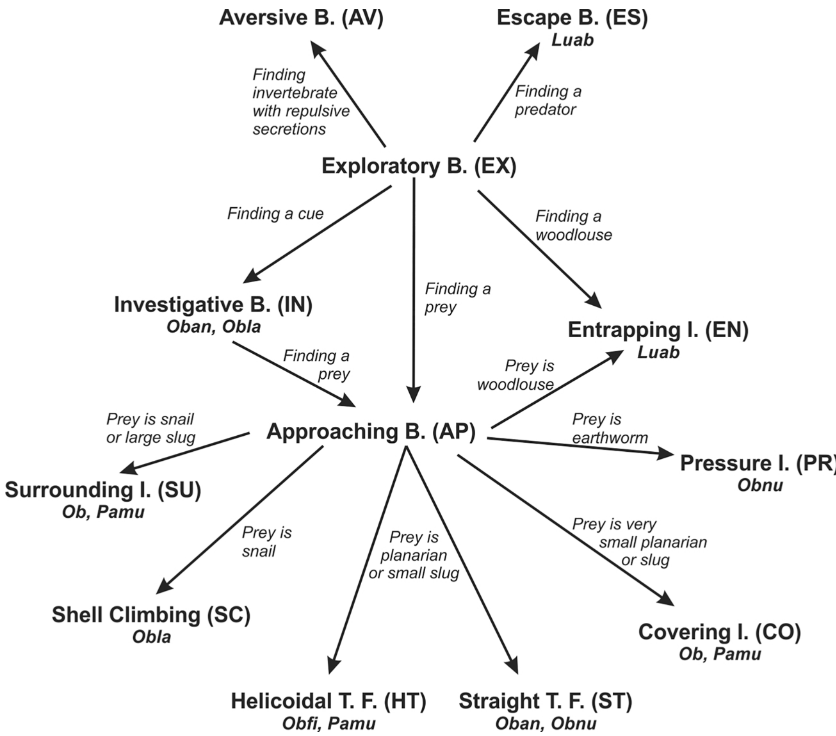

Fig. 17. Ethogram of behavioral sequences of land planarians observed during experiments of interaction with other invertebrates. Descriptions along the arrows indicate situation in which the following behavior is elicited. Abbreviations under the behavioral units indicate species in which they occur: *Luab* = *Luteostriata abundans*, *Ob* = all species of *Obama*, *Oban* = *Obama anthropophila*, *Obfi* = *Obama ficki*, *Obla* = *Obama ladislavii*, *Obnu* = *Obama nungara*, *Pamu* = *Paraba multicolor*. Abbreviations: B = Behavior; I = Immobilization; T. F. = Tube Formation.

anterior end in complex ways.

The strategy SU used by land planarians to capture gastropods seems to be common in many species that feed on these animals (Froehlich, 1955), including species distantly related to the ones in the present study, such as *Bipalium vagum*, a species originally from Southeast Asia and currently introduced in North and Central America (Ducey et al., 2007). The frequency of this behavior suggests that it is a successful strategy. The shell climbing behavior used by *O. ladislavii* seems to maximize its capture of snails and indicates that it is a species well adapted to preying on snails. In *O. ficki*, this strategy does not seem to be necessary, as its large size is enough to immobilize snails without much effort. Regarding the other species of *Obama* and *P. multicolor*, snails do not seem to make up the main item of their diet (Boll and Leal-Zanchet, 2015), thus their capture method is not very sophisticated. Froehlich's (1955) description of snail capture by land planarians indicates that other species act similarly to *O. ladislavii*.

The capture of earthworms by land planarians of the genera *Bipalium* and *Dolichoplana* seems to depend on a strong adhesion of the pharynx to the prey's surface so that even abrupt movements of the earthworm cannot free it from the planarian (Pfitzner, 1958; Zaborski, 2002). Specimens of *O. nungara* in the present study used a strategy that included stronger immobilization of the earthworm by muscle contractions, a behavior closer to the one used by the planarian *Arthurdendyus triangulatus* (Blackshaw and Stewart, 1992).

Several records indicate that woodlice are frequently used as food by land planarians (Froehlich, 1955; Barker, 1989; Carbayo, 2010). *L. abundans* is the only species that has been studied more deeply (Hauser and Maurmann, 1959; Prasniski and Leal-Zanchet, 2009) and it seems to feed exclusively on this group. The quick reaction of the planarian when contacting the prey is important for the capture of quick-moving animals such as woodlice. The detection of woodlice seems to happen especially by movement patterns, and the perception appears to be refined since other quick-moving invertebrates, such as cockroaches and ants, did not elicit a capture response by the planarian.

The interaction of *L. abundans* with *O. anthropophila* elicited an escape response, a behavior explained by the fact that *O. anthropophila* seems to be one of its main predators (Boll and Leal-Zanchet, 2016). The other five species did not show any escape behavior, so it is likely that none of the invertebrates used in the present study is a predator of any of these species. Among the few known predators of land planarians are predatory snails (Lemos et al., 2012) and carabid and staphylinid beetles (Gibson et al., 1997).

Aversive behavior was elicited during some interactions with veronicellid slugs, beetle larvae, earwigs (Dermaptera) and millipedes. Many of these invertebrates are known to have chemical defenses against predators (Cook, 1987; Gasch et al., 2013; Shear, 2015) and they may constitute the prey of land planarian species not included in the present study, as this would explain their apparent defensive behavior when facing land planarians. Veronicellid slugs were captured and eaten by some species, and millipedes are known to be the prey of certain land planarians (Terrace and Baker, 1994).

Despite their simple anatomy and strong dependence on a moist environment (Kawaguti, 1932; Carranza et al., 1998; Sluys, 1999), land planarians form a species-rich group in tropical regions and some species even succeeded in invading new habitats (Murchie and Gordon, 2013; Justine et al., 2014). The diverse set of predatory behaviors observed in the present study shows that the strategies developed by these animals are efficient and well adapted to capture a rich set of prey types in their habitats, which may help to explain their success as predators in the soil fauna.

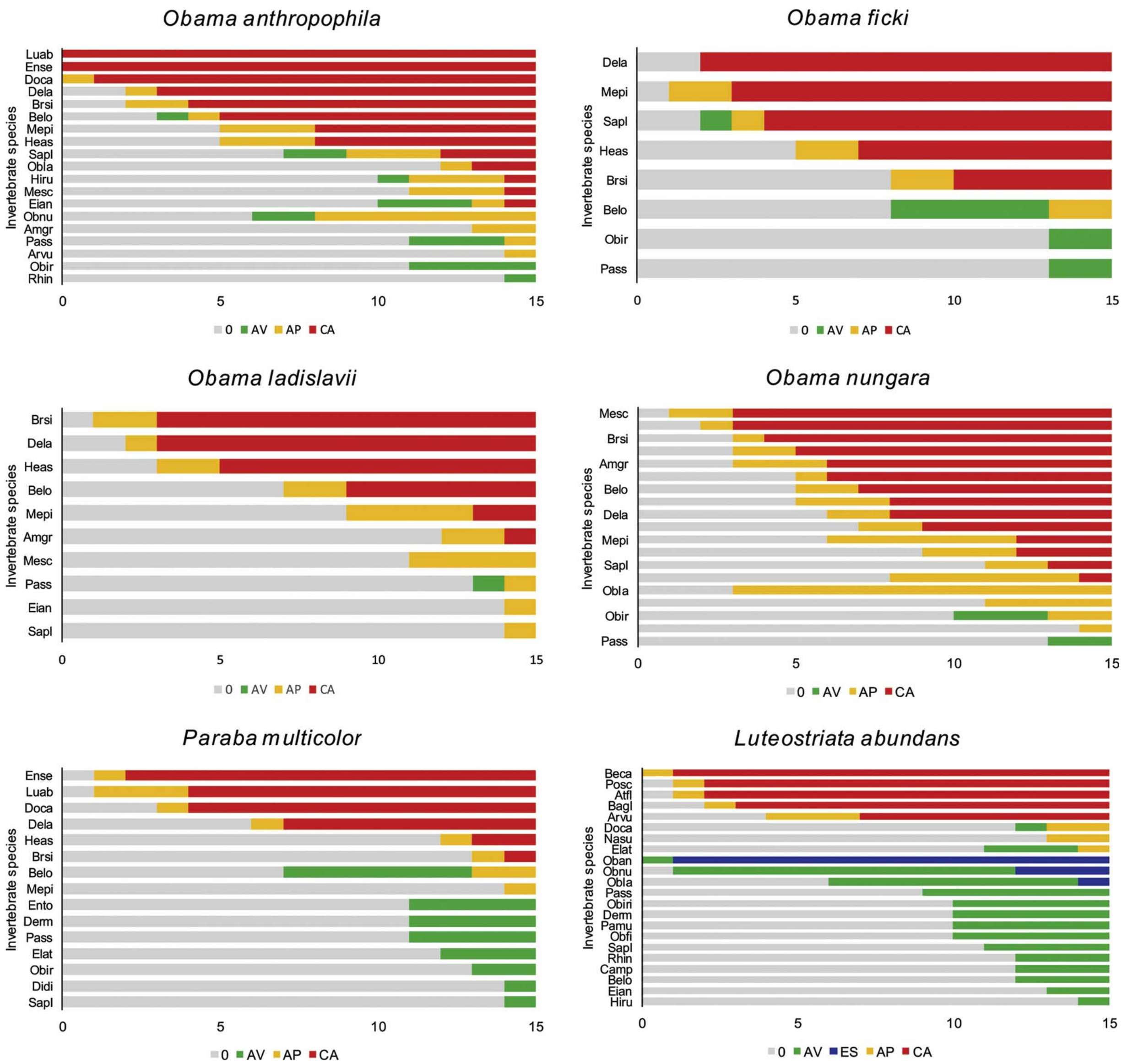

Fig. 18. Behavior of six land planarian species while interacting with different invertebrates. Abbreviations: 0 = no change; AP = approaching behavior; AV = aversive behavior; CA = capture behavior; ES = escape behavior. Abbreviations for species or other taxa: Amgr = *Amynthas gracilis*; Arvu = *Armadillidium vulgare*; Atfl = *Atlantoscia floridana*; Bagr = *Balloniscus glaber*; Beca = *Benthana cairensis*; Belo = *Belocaulus* sp.; Brsi = *Bradybaena similaris*; Camp = *Camponotus* sp.; Dela = *Deroceras laeve*; Derm = Dermaptera; Didi = *Discocyrtus* cf. *dilatatus*; Doca = *Dolichoplana carvalhoi*; Eian = *Eisenia andrei*; Elat = Elateridae; Ense = *Endeavouria septemlineata*; Ento = Entomobryidae; Heas = *Helix aspersa*; Hiru = Hirudinea; Luab = *Luteostriata abundans*; Mepi = *Meghimatium pictum*; Mesc = *Metaphire schmardae*; Nasu = *Nasutitermes* sp.; Oban = *Obama anthropophila*; Obfi = *Obama ficki*; Obir = *Obiricodesmus* sp.; Obla = *Obama ladisavii*; Obnu = *Obama nungara*; Pamu = *Paraba multicolor*; Pass = Passalidae; Posc = *Porcellio scaber*; Rhin = *Rhinocricus* sp.; Sapl = *Sarasinula plebeia*.

Table 2
Capture behavior type used by land planarians while capturing different prey species. CO = covering immobilization; EN = entrapping immobilization; HT = helicoidal tube formation; SC = shell climbing; ST = straight tube formation; SU = surrounding immobilization. Asterisks indicate exotic species.

Prey	Planarian Species					
	Obama anthropophila	*Obama ficki*	*Obama ladislavii*	*Obama nungara*	*Paraba multicolor*	*Luteostriata abundans*
*Bradybaena similaris**	SU	SU	SC	SU	SU	–
*Helix aspersa**	SU	SU	SC, SU	SU	SU	–
*Meghimatium pictum**	SU	SU	SU	SU	–	–
*Deroceras laeve**	SU	HT	SU	SU	SU	–
Sarasinula plebeia	SU	SU	–	SU	–	–
Belocaulus sp.	ST	–	CO	CO	–	–
*Eisenia andrei**	–	–	–	PR	–	–
*Amynthas gracilis**	–	–	–	PR	–	–
*Metaphire schmardae**	–	–	–	PR	–	–
Hirudinea	–	–	–	PR	–	–

(*continued on next page*)

Table 2 (*continued*)

Prey	Planarian Species					
	Obama anthropophila	*Obama ficki*	*Obama ladislavii*	*Obama nungara*	*Paraba multicolor*	*Luteostriata abundans*
*Endeavouria septemlineata**	ST	–	–	ST	CO, HT	–
Luteostriata abundans	ST	–	–	ST	HT	–
*Dolichoplana carvalhoi**	ST	–	–	ST	CO, HT	–
Obama ladislavii	ST	–	–	–	–	–
Atlantoscia floridana	–	–	–	–	–	EN
Balloniscus glaber	–	–	–	–	–	EN
Benthana cairensis	–	–	–	–	–	EN
*Porcellio scaber**	–	–	–	–	–	EN
*Armadillidium vulgare**	–	–	–	–	–	EN

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