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RESEARCH ARTICLE

Observations on food preference of Neotropical land planarians (Platyhelminthes), with emphasis on *Obama anthropophila*, and their phylogenetic diversification

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ABSTRACT. The food preference of *Obama anthropophila* Amaral, Leal-Zanchet & Carbayo, 2015, a species that seems to be spreading across Brazil's human-modified environments, was investigated. Extensive experiments led to the conclusion that the generalized diet of this species may have facilitated its dispersal. The analysis of 132 feeding records of 44 geoplaninid species revealed a tendency for closely related species to feed on individuals from similar taxonomic groups, suggesting that in this group behavioral evolution is more conserved than phylogenetic diversification.

KEY WORDS. Diet, flatworm, Geoplaninae, predation, soil fauna.

INTRODUCTION

Land planarians, or Geoplanidae (Platyhelminthes: Tricladida), are nocturnal predators that are common in humid forests (Graff 1899, Froehlich 1966, Winsor et al. 1998), although avoiding wet places (Froehlich 1955).

The general knowledge about these organisms is still far from satisfactory, especially with regards to their biology (Winsor et al.1998, 2004, Prasniski and Leal-Zanchet 2009). In part, this might owe to the fact that researchers tend to give more attention to taxonomic topics than to the behavioral aspects of their subjects (Ogren 1995). Additionally, the difficulties involved in rearing flatworms are a complicating factor (Mcdonald and Jones 2013).

Studies on the feeding preferences of land planarians have, for the most part, focused on species that are found out of their natural distribution range. They have received this kind of attention as a result of their potentially detrimental impact on native faunas. This is the case of the bipaliinids *Bipalium kewense* (Moseley, 1878), *B. adventitium* Hyman, 1943, the rhynchodeminids *Platydemus manokwari* Beauchamp, 1962, *Arthurdendyus triangulatus* (Dendy, 1894), *Endeavouria septemlineata* (Hyman, 1939) and the geoplaninid *Obama nungara* Carbayo et al., 2016 (Dindal 1970, Ducey et al. 1999, Sugiura et al. 2006, Sugiura 2009, Blackshaw 1997, Zaborski 2002, Boll and Leal-Zanchet 2015, Carbayo et al. 2016). The food preferences of the Neotropical *Obama anthropophila* Amaral, Leal-Zanchet & Carbayo, 2015, have also been studied (Boll and Leal-Zanchet 2015). The distributional area of this species was seemingly modified by human intervention within the Neotropical region, and its likely geographical areas of expansion include a northern population found at Parque Ecológico do Tietê (São Paulo, São Paulo state, Brazil). Formerly a flood plain of the Tietê River, the plain was converted into a man-created forest area in the 1970s. The nearest locality where the species is found is located ca. 500 km to the south.

Additional studies including data on the diet of native or exotic land planarians can be found in the literature. These data might provide insights on the food preferences of congeners, even though their diet has not been addressed yet.

In the present study, (a) further experiments were carried out to study the diet preferences of the northern population of *O. anthropophila*, and (b) data on their diet was compiled from field and laboratory observations, as well as from the literature, and mapped onto a genus-level classification of land planar-

ians of the subfamily Geoplaninae, in order to evaluate the behavioral evolution of these animals during their phylogenetic diversification.

MATERIAL AND METHODS

We focused on land planarians of the subfamily Geoplaninae. Data on their diet were obtained from three sources: (a) sets of trials and experiments under laboratory conditions using *O. anthropophila*, (b) our own occasional observations in nature and under laboratory conditions, and (c) published literature.

Nineteen specimens of *O. anthropophila* were collected during the day between May, 2011 and February, 2012, from the Parque Ecológico do Tietê, in the city of São Paulo, state of São Paulo, Brazil (23°29'06"S 46°31'12"W). The 1400 ha. park is a managed area comprised of meadows, patches of flowers and trees, mainly exotic species. At the time of capture, most individuals were photographed with a digital camera and the length of each specimen was measured. Each specimen was then placed in a labeled cylindrical plastic container with a cotton ball moistened with mineral water, and 2-3 pieces of tree bark for refuge. The containers measured either 10 x 5 cm (diameter x height) (those were allocated for specimens less than 2 cm long), or 11 × 7 cm (allocated for specimens larger than 2 cm). The containers were kept in a cardboard box to provide darkness, at room temperature and humidity, in the Laboratório de Ecologia e Evolução. The containers were cleaned twice a week, with the cotton balls substituted with fresh ones. Five different species of invertebrates that are abundant at the sampling site and coexist with *O. anthropophila*, were offered as potential prey. Some prey were known to be food items of *O. anthropophila* (land planarians and mollusks) (Froehlich 1956, Boll et al. 2015), whereas other prey had not been previously recorded as such (Diplopoda). Prey that could not be identified at the species level was identified by its common name and at a higher taxonomic level.

In order to stimulate readiness to feed (Sugiura 2009), specimens were starved for seven days (in a few cases four days) between one set of trials and the next. A trial consisted of putting a specimen of *O. anthropophila* and a potential prey item together in a 9-14 cm diameter glass Petri dish dampened with a few drops of mineral water. The trials were conducted separately, during the day, and at room temperature, with all available flatworms. In each case, a specimen of any one of the following five potential prey species was offered: diplopods (Arthropoda), slugs (Limacidae, Mollusca), and individuals from three geoplaninid land planarian species, *Issoca rezendei* (Schirch, 1929), *Geoplana quagga* Marcus, 1951 and *Luteostriata ernesti* (Leal-Zanchet & Froehlich, 2006). Interest in the prey was observed and recorded for 30 minutes (Sony Handycam HDR – XR550V camcorder). Feeding was assumed to have occurred if the prey was either totally or partially ingested. If there was no interest, the same procedure was repeated with the same flatworm and a second

Table 1. Survival and predation rate (indicated as preyed/offered) of 19 specimens of *Obama anthropophila* when fed with one out of five different types of prey species under laboratory conditions. A specimen not given as prey is indicated with a hyphen. See Material and Methods for details.

Specimen identification	Specimen survival (days)	*Issoca rezendei* (Geoplaninae)	*Luteostriata ernesti* (Geoplaninae)	*Geoplana quagga* (Geoplaninae)	*Deroceras laeve* (Gastropoda)	*Millipede* (Diplopoda)	# trials
A	150	3/6	1/2	2/6	2/6	0/5	25
C	76	4/6	1/2	1/5	1/2	0/3	18
B	50	2/3	0/1	1/2	2/3	0/2	11
D	50	2/3	2/2	1/3	0/1	0/1	10
X	89	1/2	0/1	–	1/1	0/1	5
J	6	0/1	0/1	0/1	0/1	0/1	5
E	20	0/1	0/1	0/1	0/1	0/1	5
Alpha	70	0/1	2/2	–	–	0/1	4
P	13	0/1	–	0/1	0/1	0/1	4
Z	19	1/1	1/1	–	0/1	–	3
N	?	1/1	–	0/1	–	–	2
B2	20	1/1	0/1	–	–	–	2
B1	19	0/1	–	0/1	–	–	2
O	6	1/1	–	–	–	–	1
L	6	–	–	–	1/1	–	1
I	6	–	1/1	–	–	–	1
H	~20	1/1	–	–	–	–	1
G	20	–	–	1/1	–	–	1
F	~20	–	–	–	1/1	–	1
		56.7% (17/30)	53.3% (8/15)	27.3% (6/22)	42.1% (8/19)	0.0% (0/16)	102

potential prey by another species. If the situation persisted, the procedure was repeated again and again until all five potential prey items had been offered. In case of ingestion, the trial was considered completed, and no further offerings were made on the same day. The flatworm was then returned to the darkened container. In the first trial, the sequence of prey offerings was always as follows: a millipede, the slug *Deroceras laeve* (Müller, 1774), and then sequentially three land planarians, *I. rezendei*, *G. quagga*, and *L. ernesti*. A set of trials was considered concluded after the fifth offering was completed, or when prey had been ingested. The following week, a new set of trials took place with all flatworms available; first by offering the second prey of the above-established sequence, followed by the third, fourth, fifth and first, in this sequence. One hundred and two trials were performed in this manner. With the exception of one specimen, the number of days each snail survived in the lab was registered (Table 1). Causes of death were not investigated in this study.

Additionally, 25 experiments involving *O. anthropohila* with ten different options of prey were carried out. In this case, flatworms that had survived previous trials were starved for 10 days before being offered prey, in accordance with the established procedure.

A summary was compiled with the available diet records and prevailing conditions of diet, both from our own field and lab notes taken since the 1950s (Tables 2, 3), as well as from the literature (Suppl. material 1, 2). Our field notes were originated from several encounters with flatworms feeding on prey. Laboratory notes refer to anecdotal feeding experiments conducted with land flatworms prior to killing them for taxonomic studies. Such experiments consisted of putting a flatworm specimen together with an available potential prey item (which had been found nearby in the field) on a Petri dish or in a small box, followed by an observation of its behavior for 1-5 minutes. If the planarian displayed interest in the prey by attacking it and protruding the pharynx, the prey was taken away for further identification and was considered a food item. In most cases, anecdotal experiments were conducted just once with a land planarian species. Temperature, humidity or times of the day were not controlled.

Table 2. Feeding preferences of species of Geoplaninae land planarians presented here for the first time. Observation conditions, either in nature (nat) or in the laboratory (lab), and references are given in brackets; a hyphen indicates observation conditions as unavailable.

Land flatworm species	Invertebrate consumed
Cephaloflexa bergi (Graff, 1899)	Harvestman *Progonyleptoidellus striatus* (Roewer, 1913) (Gonyleptidae, Opiliones) [lab]
	Harvestman *Neosadocus* sp. (Gonyleptidae, Opiliones) [nat]
	Harvestman *Mischonyx cuspidatus* (Roewer, 1913) (Gonyleptidae, Opiliones) [lab]
	Unidentified insect larva [nat]
	Unidentified harvestman (Fig. 4) [nat]
	Cricket *Gryllus* sp. (Orthoptera, Insecta) [lab]
Cephaloflexa bergi (Graff, 1899)	Unidentified woodlice (Oniscidea, Crustacea) [-]
	Larva of *Tenebrio* sp. (Coleoptera) [lab]
Geobia subterranea Schultze & Müller, 1857	Unidentified earthworm (Oligochaeta, Annelida) [nat] (Fig. 5)
Geoplana beckeri Froehlich, 1959, incertae sedis	Unidentified earthworm (Oligochaeta, Annelida) [-]
Geoplana cf. *chita* Froehlich, 1956	Unidentified land snail (Gastropoda) [nat] (Fig. 6)
Geoplana goetschi Riester, 1938 incertae sedis	Unidentified land leech (Hirudinea, Annelida) [nat]
	Torn land slug *Limax* sp. (Gastropoda) [lab]
Geoplana quagga Marcus, 1951, incertae sedis	Land planarian *Dolichoplana striata* Moseley, 1877 (Geoplanidae) [lab]
	Unidentified woodlice (Oniscidea, Crustacea) [lab]
Imbira marcusi Carbayo et al., 2013	Unidentified earthworm (Oligochaeta) [nat] (Fig. 7)
Issoca rezendei (Schirch, 1929)	Unidentified woodlice (Oniscidea, Isopoda) [lab]
Luteostriata caissara (E. M. Froehlich, 1955)	Unidentified woodlice (Oniscidea, Isopoda) [lab]
Luteostriata ernesti (Leal-Zanchet & E. M. Froehlich, 2006)	Unidentified woodlice (Oniscidea, Isopoda) [lab]
Luteostriata sp.	Unidentified woodlice (Oniscidea, Isopoda) [lab]
Notogynaphallia plumbea (Froehlich, 1959)	Unidentified larva of an insect [nat]
Notogynaphallia sexstriata (Graff, 1899)	Insecta: larva of an insect [nat] (Fig. 8)
Obama anthropophila Amaral, Leal-Zanchet & Carbayo, 2015	Land planarian *Issoca rezendei* (Schirch, 1929) (Geoplanidae) [lab] (Fig. 1, Suppl. material 1)
	Land planarian *Luteostriata ernesti* (Leal-Zanchet & Froehlich, 2006) (Geoplanidae) [lab] (Suppl. material 1)
	Land planarian *Geoplana quagga* Marcus, 1951, (Geoplanidae) [lab]
	Land planarian *Geobia subterranea* Schultze & Müller, 1857 (Geoplanidae) [lab] (1/2)
	Land planarian *Endeavouria septemlineata* (Hyman, 1939) (Geoplanidae) [lab] (1/4)
	Unidentified Terrestrial ribbon worm (Nemertea) [lab] (1/1)
	Land slug *Bradybaena similaris* (Gastropoda) (1/2)
	Land slug *Deroceras laeve* (Müller, 1774) (Gastropoda) [lab] (Suppl. material 1)
	Land snail *Bradybaena similaris* (Férussac, 1821) (Gastropoda) [lab]
Obama burmeisteri (Schultze & Müller, 1857)	Land snail *Achatina fulica Bowdich*, 1822 (Gastropoda) [nat] (Fig. 2)
	Land slug *Bradybaena similaris* (Férussac, 1821) (Gastropoda) [lab]
Obama baptistae (Oliveira & Leal-Zanchet, 2012)	Land snail (Gastropoda) [lab]
	Land snail (Gastropoda) [lab]
Obama carinata (Riester, 1938)	Land slug Veronicellidae (Gastropoda) [lab, nat] (Fig. 3)
Obama evelinae (Marcus, 1951)	Unidentified land snail [nat] (Fig. 9)
Obama ferussaci (Graff, 1897)	Land planarian *Cephaloflexa bergi* (Graff, 1899) (Geoplanidae) [nat]
Paraba franciscana (Leal-Zanchet & Carbayo, 2001)	Unidentified land leech (Hirudinea, Annelida) [nat]
Paraba phocaica (Marcus, 1951)	Land snail *Happia* sp. (Systrophiilidae, Gastropoda) [nat]
Pasipha tapetilla (Marcus, 1951)	Unidentified millipede [nat]

Figures 1–9. Photographs of land planarians feeding under laboratory conditions (1) and in nature (2–9). Orange arrowheads point to prey; blue arrowheads point to the predator flatworm. (1) *Obama anthropophila* capturing *Issoca rezendei*. Note the body margins bending onto the prey, thus preventing it from escaping even before being eaten (inset); (2) a young specimen of *Obama burmeisteri* feeding on the giant African snail (Ilhabela, SP); (3) *Obama carinata* handling a slug (Veronicellidae) (Parque Estadual da Serra da Cantareira, São Paulo, SP); (4) *Cephaloflexa bergi* eating a harvestman (Reserva Biológica Augusto Ruschi, ES); (5) *Geobia subterranea* eating an earthworm (Caxambu, MG); (6) *Geoplana* cf. *chita* disturbed while eating a snail to show the shell (São Sebastião, SP); (7) two specimens of *Imbira marcusi* simultaneously attacking an earthworm (Parque Estadual Intervales, SP); (8) *Notogynaphallia* cf. *sexstriata* eating an insect larva (Parque Estadual da Serra do Mar, SP); (9) *Obama evelinae* eating a land snail (Reserva Natural Municipal Nascentes de Paranapiacaba, Santo André, SP).

RESULTS

Specimens of *O. anthropophila* survived up to 150 days under laboratory conditions (median 20 days; range 6–150 days; Table 1). Four out of the five different types of prey in the initial trials were ingested: the three geoplaninids, and the gastropod. The millipede was always rejected. Predation rate varied from 56.7% (*I. rezendei*, Fig. 1) to 27.3% (*Geoplana quagga*) (Table 1; Suppl. material 3). In the additional experiments, *O. anthropophila* also accepted two additional species of Geoplaninae (*Geobia subterranea* Schultze & Müller, 1857, and *Endeavouria septemlinetata* (Hyman, 1939), a ribbon worm (Nemertea) and an exotic gastropod (*Bradybaena similaris* (Ferussac, 1821)) (Table 2). In constrast, it rejected one species of land planarian (*Obama burmeisteri* (Schultze & Müller, 1857)), and one species each of veronicellid gastropods, millipedes, woodlice, Mycetophilidae larva, and Microlepidoptera and earthworm larvae, respectively (Table 3).

Data were obtained on the diets of 44 species of Geoplaninae. A total of 132 records (45 new, Tables 1, 2; 87 from the literature, Suppl. material 1) account for the consumed prey, and

Table 3. Invertebrates not eaten by species of Geoplaninae land planarians in laboratory conditions, presented here for the first time. If available, number of experiments is given in parentheses.

Land flatworm species	Invertebrate not eaten
Geoplana quagga Marcus, 1951, incertae sedis	Unidentified woodlice (Oniscidea, Crustacea)
	Unidentified millipede (Diplopoda)
	Unidentified springtail (Collembola, Hexapoda)
	Unidentified earthworm (Oligochaeta)
	Unidentified ant (Formicidae, Insecta)
	Unidentified land snail (Gastropoda)
Imbira marcusi Carbayo et al., 2013	Unidentified land snail (Gastropoda)
	Unidentified springtail (Collembola, Hexapoda)
	Unidentified earthworm (Oligochaeta)
Issoca rezendei (Schirch, 1929)	Unidentified land snail (Gastropoda)
	Unidentified torn slug (Gastropoda)
	Unidentified torn springtail (Collembola, Hexapoda)
	Unidentified millipede (Diplopoda)
	Unidentified ant (Formicidae, Insecta)
Luteostriata ernesti (Leal-Zanchet & E. M. Froehlich, 2006)	Unidentified land snail (Gastropoda)
	Unidentified torn springtail (Collembola, Hexapoda)
	Unidentified earthworm (Oligochaeta)
	Unidentified millipede (Diplopoda)
	Unidentified land slug (Veronicellidae, Gastropoda)
	Unidentified earthworm (Oligochaeta)
	Unidentified woodlice (Oniscidea, Crustacea)
	Unidentified millipede (Diplopoda)
Obama anthropophila	Unidentified larva of Mycetophilidae (Insecta)
	Unidentified larva of Microlepydoptera (Insecta)
	Land planarian Obama burmeisteri (Schultze & Müller, 1857) (4)
	Unidentified Veronicellidae (Gastropoda) (1)
	Unidentified larva of Microlepidoptera (Insecta) (1)
	Unidentified larva of Mycetophilidae (Insecta) (1)
	Unidentified land isopod (Oniscidea) (3)
	Unidentified earthworm (Oligochaeta) (4)
Obama braunsi (Graff, 1899)	Unidentified earthworm (Oligochaeta)
	Unidentified woodlice (Oniscidea, Crustacea)
Obama burmeisteri (Schultze & Müller, 1857)	Unidentified woodlice (Oniscidea, Crustacea)
	Unidentified ant (Formicidae, Insecta)
Obama nungara Carbayo, Álvarez-Presas, Jones & Riutort, 2016	Unidentified, very juvenile land snail (Helicidae, Gastropoda)
Pasipha pasipha (Marcus, 1951)	Unidentified land snail (Gastropoda)
	Unidentified earthworm (Oligochaeta)
	Unidentified woodlice (Oniscidea, Crustacea)
	Unidentified ant (Formicidae, Insecta)
	Unidentified earthworm (Oligochaeta)
	Unidentified torn land slug (Gastropoda)
Xerapoa pseudorhynchodemus (Riester, 1938)	Unidentified land snail (Gastropoda)
	Unidentified springtail (Collembola, Hexapoda)
	Unidentified millipede (Diplopoda)
	Unidentified ant (Formicidae, Insecta)

244 records mention prey that were not eaten (46 new, Tables 1, 3; 198 from literature, Suppl. material 2).

Nine species of *Obama* predate on gastropods, and six on other land flatworms. However, *O. anthropophila* preyed upon nine species across three phyla, including three introduced species, *Deroceras laeve* (Müller, 1774) from North America (Hammond 1996), *Bradybaena similaris* (Férussac, 1821) from Asia (Carvalho et al. 2008) and *E. septemlineata*, probably from Hawaii (Hyman 1939) (Tables 1, 2). Interestingly, according to anecdotal observations (see Table 3), *O. carrierei*, *O. carrierei* var. brownish, *O. ferussaci*, *O. josefi* and *O. trigueira* only prey on other geoplaninids (Tables 2, Suppl. material 1) as observed by Boll and Leal-Zanchet (2016).

Matuxia tuxaua (E.M. Froehlich, 1955) and *M. matuta* (E.M. Froehlich, 1955) feed on beetle larvae, and four species of *Luteostriata* as well as *I. rezendei* feed exclusively on woodlice, rejecting any other kind of prey (Prasniski and Leal-Zanchet 2009; Tables 2, Suppl. material 2).

Two species of *Cephaloflexa* feed on harvestmen, while one of them, *C. bergi*, also takes other arthropods, such as Diptera and woodlice (Tables 2, Suppl. material 1). Three species of *Xerapoa* consume small arthropods (Suppl. material 1). Finally, *Geoplana* cf. *vaginuloides* (Darwin, 1844) and *G.* cf. *chita* (E.M. Froehlich, 1956), two of three taxonomically well-established species of *Geoplana* (*G. pulchella* is the third), prey on snails (Tables 2, Suppl. material 1).

DISCUSSION

Apparently, geoplaninids prey on a wide range of taxonomic groups, including snails, slugs (Mollusca: Gastropoda), acari, harvestmen (Arthropoda: Arachnida), woodlice (Arthropoda: Crustacea), adult and larval stages of insects (Arthropoda: Hexapoda), land planarians (Platyhelminthes: Tricladida), land leeches, earthworms (Annelida: Oligochaeta), and terrestrial ribbon worms (Nemertea). Some land flatworm species only feed on organisms of one taxonomic group (e.g., Gastropoda, Opiliones), whereas others display wider diet breadth. The former are called 'specialists', and the latter 'generalists', according to the Ali and Agrawal (2012) grouping of insect herbivores.

Generalist species

Obama anthropophila is a generalist predator. In addition to preying on thirteen species across three phyla, Platyhelminthes, Nemertea, and Mollusca, its diet also includes exotic species. Boll and Leal-Zanchet (2016) recorded slugs and land planarians as prey of a population of this species from South Brazil. Our results agree with their observations and expand our knowledge on the food preferences of *O. anthropophila*, thereby suggesting high food plasticity.

Only a few other flatworms are known to be generalists. The New Guinea rhynchodeminid, *Platydemus manokwari* preys

on mollusks, earthworms, woodlice, flatworms and terrestrial ribbon worms (Sugiura 2009), while *E. septemlineata* feeds on earthworms, small insects, snails and slugs (Winsor et al. 2004). *Obama nungara* is able to ingest organisms that are covered with mucus or chitin (Carbayo et al. 2016). The generalist predatory behavior of these land planarians possibly favors successful colonization of non-native areas. Although these three species are encountered under these conditions, the extent to which their success is enhanced by their generalist diet remains to be studied. The microplanid *Microplana terrestris* (Müller, 1774), mainly a scavenger, also feeds on a variety of organisms such as earthworms, slugs, woodlice and millipedes (see Mcdonald and Jones 2013). Although this species is widely distributed across Europe (Mcdonald and Jones 2013), to date there is no indication of its spread being human-mediated.

Diet breadth tends to be restrained within genera

The results summarized in this work suggest that the diets of closely related species, i.e., species of the same genus, tend to be similar. In a study of mollusk predation by land planarians, Winsor et al. (2004) failed to notice any evident trend across "the generalist-specialist spectrum in behavioral or structural traits associated with handling prey". However, knowledge has accumulated on the diets of species from *Luteostriata*, *Cephaloflexa* and *Obama*. Furthermore, a sound classification of most geoplaninid genera is also currently available (Carbayo et al. 2013). Thus, hypotheses relating feeding behavior with phylogeny can now be formulated.

In species of *Luteostriata*, prey capture is facilitated by the combined action of sticky mucus secretion and the sucker-like action of the ventral side of the cephalic extremity (Hauser and Maurmann 1959, Prasniski and Leal-Zanchet 2009). Capture of woodlice by its close relative *I. rezendei* (see Carbayo et al. 2013) is similar (MC Ramos, unpublished data). The cutaneous longitudinal-ventral muscle fibers of all the species of this clade are disposed to be fan-like, thereby giving rise to a cephalic retractor muscle. This retractor differs in detail among the genera, varying in fiber organization, and with participation of additional cutaneous and parenchymatic muscle fibers (Froehlich 1955, Carbayo and Leal-Zanchet 2003, Carbayo 2010). The ventral side of the cephalic region is pierced by numerous glands, which, at least in the case of *Issoca*, function as suckers. Furthermore, in this genus, the contraction of cephalic muscles accentuates the concavity of the ventral side, which is sucker-like and aided by mucus secretion, to hold the prey (Froehlich 1955). As various specimens of non-woodlice prey were rejected by species of *Issoca* and *Luteostriata* (Table 3), it is presumed that woodlice are the principal item in the diet of all species of *Luteostriata*, *Issoca* and *Supramontana*.

To date, *Cephaloflexa bergi*, *C. araucariana* and *Choeradoplana crassiphalla* Negrete & Brusa, 2012, are the only planarian species known to feed on harvestmen. Interestingly, these two genera are sister groups. When crawling, the anterior extremity of these flatworms is curled up (Marcus 1951, Carbayo and Leal-Zanchet 2003). In nature, specimens of *C. bergi* have been observed preying on harvestmen five times. Under laboratory conditions, by contrast, this has been recorded several times. When the flatworm detects the harvestman at close quarters, its cephalic extremity is unrolled and thrust towards the prey, which adheres to the tip of the body. The prey is most often consumed right thereafter.

Species of *Choeradoplana* and *Cephaloflexa* also show cephalic muscle specializations, but unlike *Luteostriata* and close relatives, the muscle fibers of the retractor run ventrally along the antero-posterior axis of the body. In this respect, *Choeradoplana* and *Cephaloflexa* differ from each other in some morphological details (see details in Froehlich 1955, Carbayo and Leal-Zanchet 2003). In species of *Choeradoplana* and *Cephaloflexa*, the epidermis of the cephalic region is traversed by various types of glands, some of which are adhesive. This combination of cephalic muscles and adhesive secretion most likely facilitates prey capture. Muscle contractions presumably induce quick unrolling of the anterior extremity, thereby placing the sticky ventral surface in rapid contact with the prey. It is hypothesized that this characteristic muscular and glandular specialization makes all species of *Choeradoplana* and *Cephaloflexa* prefer harvestman as a food source.

Most species of *Obama* prey on gastropods (Tables 1-3). These flatworms have a large, wide and flat body. In the laboratory, *O. anthropophila* (Fig. 1, video as Supplementary Material 3), *O. baptistae*, *O. braunsi*, *O. burmeisteri* (Fig. 2), *O. carinata* (Fig. 3), *O. ladislavii* and *O. nungara* have been observed handling gastropods with their body (Boll and Leal-Zanchet 2015). The worm bends the edges of the body downwards, so as to embrace the prey and press it against the soil, thus preventing escape. The wide-body feature is apparently favorable for handling snails and slugs. Hence, hypothetically the flat and wide-bodied *Obama* species should prefer terrestrial gastropods. Boll and Leal-Zanchet (2016) suggested that the differences in the diet among species of the genus decrease food competition and facilitate their coexistence.

The wide diet breath of these snails might facilitate their dispersal by humans and their subsequent colonization of new habitats. For instance, the generalist species *O. anthropophila* and *O. nungara* have colonized new habitats. Conversely, *O. ladislavii* is a diet-specialist that has a relatively great potential to become an invasive species, since it is tolerant to variation in environment (Boll and Leal-Zanchet 2016).

Finally, despite the non-quantitative nature of the records, the food preferences of species within the genera *Geoplana*, *Matuxia* and *Xerapoa*, reinforce the hypothesis that diet specializations happens within the taxonomic groups of snails, insect larvae and arthropods, respectively (Tables 1–3).

Although our observations should simply be considered as working hypotheses, they seem to support the idea that "ecological and behavioral change in geoplaninids is more conservative than phylogenetic diversification," as pointed

out by Brooks and McLennan (1991: 344-345) for a variety of taxonomic groups. In other words, the systematic classification of geoplaninids may have predictive power regarding their food preferences. *Obama anthropophila*, in contrast, is a generalist. This might have been a beneficial factor in facilitating its successful colonization of regions outside of its natural distribution area within the Neotropical region.

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Supplementary material 1

Table S1. Invertebrate consumed by Geoplaninae land planarians

Authors: Amanda Cseh, Fernando Carbayo, Eudóxia Maria Froehlich

Data type: species data

Supplementary material 2

Table S2. Invertebrate not eaten by Geoplaninae land planarians in lab conditions

Authors: Amanda Cseh, Fernando Carbayo, Eudóxia Maria Froehlich

Data type: species data

Supplementary material 3

Video of food preference of Neotropical land planarians

Authors: Amanda Cseh, Fernando Carbayo, Eudóxia Maria Froehlich

Data type: video observation

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