

## **Biology and Control of the Leatherleaf Slug *Leidyula floridana* (Mollusca: Gastropoda: Veronicellidae)**

Authors: Capinera, John L., and Rodrigues, Cleiton Guedes

Source: Florida Entomologist, 98(1) : 243-253

Published By: Florida Entomological Society

URL: <https://doi.org/10.1653/024.098.0141>

---

The BioOne Digital Library (<https://bioone.org/>) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (<https://bioone.org/subscribe>), the BioOne Complete Archive (<https://bioone.org/archive>), and the BioOne eBooks program offerings ESA eBook Collection (<https://bioone.org/esa-ebooks>) and CSIRO Publishing BioSelect Collection (<https://bioone.org/csiro-ebooks>).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](http://www.bioone.org/terms-of-use).

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

# Biology and control of the leatherleaf slug *Leidyula floridana* (Mollusca: Gastropoda: Veronicellidae)

John L. Capinera and Cleiton Guedes Rodrigues

---

## Abstract

*Leidyula floridana* (Leidy, 1851) (Mollusca: Gastropoda: Veronicellidae), also known as Florida leatherleaf slug, has long been known to be a pest of ornamental plants in southern Florida, and of food crops in the Caribbean region. Its geographic range is expanding, and it also has become an intermediate host for the nematode *Angiostrongylus cantonensis* (Chen, 1935) (Strongylida: Metastrongylidae), which can cause meningoencephalitis in humans and other primates if ingested. Thus, it is increasingly important that we understand its biology and management. We determined that about 50% survived more than 18 mo under laboratory conditions. It attained a maximum mean weight of about 13.4 g after 18 mo, but individuals as large as 28.5 g were occasionally obtained in our cultures. It burrowed in the soil or sought shelter during the daylight hours. Slugs began egg production when 3-7 g in weight, and deposited clusters of about 45 oval eggs in or atop the soil. Eggs measured about 7.4 mm in length and 4.8 mm in width, and commonly were produced by slugs 150-350 days after hatching. Older slugs, for the most part, seemed to be post-reproductive. Eggs hatched after about 2 weeks of incubation at 26°C. Slugs burrowed into moist soil ( $\geq 50\%$  of soil moisture capacity) in preference to drier soil. When newly hatched slugs were fed various potential foods, they grew well on some vegetables and weeds, but not all. The ornamental plants evaluated were less suitable, as were miscellaneous materials such as mushrooms and animal feces. However, most materials allowed the slugs to survive for over 30 d, and if they were provided with suitable food thereafter, they commenced rapid growth. Larger slugs readily consumed the host plants suitable for growth of young slugs, and consumed measurable quantities of about 80% of the plant species presented. Thus, this species is very resilient, and many organic materials will allow them to survive protracted periods. The amount of leaf tissue consumed per day by this slug increased with size (age) until attaining a mean slug weight of about 8 g, then the rate of consumption tapered off. In the case of Romaine lettuce, average foliage consumption peaked at about 15-20 cm<sup>2</sup> per day. The relative consumption rate (cm<sup>2</sup>/g/day) declined with age throughout development. We tested 4 commercial snail and slug bait products for comparative effectiveness. The metaldehyde-, iron phosphate-, and sodium ferric EDTA-containing baits all induced significant levels of mortality, though the metaldehyde-containing bait induced mortality more quickly and resulted in a higher level of mortality. All 3 of these baits arrested foliage consumption. The orthoboric acid bait did not induce mortality or affect consumption, apparently because the bait substrate of this product was not eaten by the slugs. Neem oil, which has been reported to be a phagostimulant for the snail *Zonitoides arboreus*, did not affect consumption of orthoboric acid bait or foliage.

Key Words: life history; host plant selection; host plant suitability; molluscicides

## Resumen

*Leidyula floridana* (Leidy, 1851) (Mollusca: Gastropoda: Veronicellidae), conocido como la babosa de hoja de cuero de Florida también, durante mucho tiempo ha sido conocida como una plaga de plantas ornamentales en el sur de Florida y de cultivos alimenticios en la región del Caribe. Su área de distribución geográfica se está expandiendo, y se ha convertido en un hospedero intermedio para el nematodo *Angiostrongylus cantonensis* (Chen, 1935) (Strongylida: Metastrongylidae), que, si se ingiere, puede causar meningoencefalitis en humanos y otros primates. Por lo tanto, cada vez es más importante que comprendamos su biología y manejo. Se determinó que esta babosa vive por un largo tiempo, con aproximadamente el 50% sobreviviendo más de 18 meses bajo condiciones de laboratorio. Esta alcanzó un promedio máximo de peso de alrededor de 13.4 g después de 18 meses, pero habían individuos tan grandes como de 28.5 g ocasionalmente en nuestras culturas. Se escavaron en el suelo o buscaron refugio durante las horas de luz. Las babosas comenzaron la producción de huevos cuando tenían 7.3 g de peso y depositaron grupos de unos 45 huevos ovalados en o encima del suelo. Los huevos midieron aproximadamente 7.4 mm de longitud y 4.8 mm de ancho y usualmente fueron producidos por babosas de 150-350 días después de la eclosión. Las babosas mayores, en su mayor parte, parecían ser pos-reproductiva. Los huevos eclosionaron después de casi 2 semanas de incubación a los 26 °C. Las babosas escavaron en el suelo húmedo ( $\geq 50\%$  de la capacidad de la humedad del suelo) con una preferencia a suelo más seco. Cuando se alimentó a las babosas recién eclosionados con varios alimentos potenciales, crecieron mejor sobre verduras como la lechuga romana, calabaza Seminole, okra y frijol. Algunas malezas también favorecieron el crecimiento, especialmente el Pusley de Florida y la poinsettia salvaje, pero también la maleza mendiga de Florida, la flor de diamantes del Viejo Mundo y la escobilla cubana. Las plantas ornamentales evaluadas fueron menos adecuadas, al igual que materiales diversos, tales como los champiñones y las heces de animales. Sin embargo, las babosas sobrevivieron por más de 30 días sobre la mayoría de los materiales, y si luego se les proporcionaba comida adecuada, ellas comenzaron un rápido crecimiento. Por lo tanto, esta especie es muy resistente, y muchos materiales orgánicos les permitirá sobrevivir períodos prolongados sin plantas alimenticias adecuadas. La cantidad de tejido foliar consumida por día por esta babosa aumentó con el tamaño

---

Entomology & Nematology Department, University of Florida, Gainesville, FL 32611, USA

\*Corresponding author; E-mail: Capinera@ufl.edu

(edad) hasta que se alcanzó un promedio de peso de babosa de aproximadamente 8 g y luego su consumo se disminuyó. En el caso de la lechuga romana, el promedio de follaje consumido alcanzó un máximo de alrededor de 15-20 cm<sup>2</sup> de tejido de las hojas por día. La tasa de consumo relativo (cm<sup>2</sup> /g/ día) disminuyó con la edad durante todo el desarrollo. Las babosas más grandes consumieron fácilmente las plantas hospederas adecuadas para el crecimiento de las babosas jóvenes, y se consumen cantidades medibles de alrededor del 80% de las especies de plantas que se presentan. Probamos la efectividad comparativa de cuatro productos de cebos comerciales para caracoles y babosas. Todos los cebos que contienen metaldehído, fosfatos de hierro y EDTA férrico de sodio indujeron niveles significativos de mortalidad, aunque el cebo que contiene metaldehído indujo la mortalidad más rápidamente y resultó en un nivel más alto de mortalidad. Los tres cebos detuvieron el consumo de follaje. El cebo que contenía ortoborato no indujo la mortalidad ni afectó el consumo, aparentemente porque el sustrato del cebo de este producto no fue comido por las babosas. El aceite de neem, que ha sido reportado como un fagoestimulante para la caracol *Zonitoides arboreus*, no afectó el consumo del cebo de ortoborato o del follaje.

Palabras Clave: historia de vida; selección de plantas hospederas; idoneidad de planta hospedera; molusquicidas

The family Veronicellidae (Gray, 1840) consists of morphologically distinct slugs generally known as leatherleaf slugs. Unlike most slugs, they are flattened, and the entire body is covered with a thick mantle. This family consists of about 20 genera, including about 100 species (Thomé 1989; Gomes 2007). Veronicellid slugs are largely tropical and subtropical in distribution, and most diverse in the Americas and Africa, although some occur in Asia and Australia (Barker 2001, Gomes & Thomé 2004). They display hermaphroditic reproduction, and nearly all are oviparous. They are herbivorous and detritivorous, and often burrow in the soil during the daylight hours. Some species are important crop pests, damaging such plants as coffee, banana, tobacco, pepper, tomato, and especially bean (Rueda et al. 2002).

These species are important as intermediate hosts of nematodes, especially *Angiostrongylus cantonensis* (Chen, 1935) (Strongylida: Metastrongylidae) and *A. costaricensis* (Diaz 2010; Wang et al. 2008; Rueda et al. 2002). Consumption of molluscs containing *A. cantonensis* can cause eosinophilic meningoencephalitis in primates, and consumption of *A. costaricensis* Morera & Cespedes, 1971 can cause abdominal angiostrongylosis in humans. *Angiostrongylus cantonensis* has also been detected in the mucus secretions (slime) of slugs (Qvarnstrom et al. 2007), suggesting another possible route of human infection, as slugs leave behind a trail of mucus as they travel, and this could be ingested if they climb onto vegetable plants.

The most commonly encountered veronicellid found in the USA is *Leidyula floridana* (Leidy, 1851), also known as the Florida leatherleaf slug. As suggested by its specific name, it was originally described from Florida. However, it likely originated in Cuba (Pilsbry 1948), where it is widespread (Maceira 2003), and also occurs on other islands of the Antilles. Formerly limited in the USA to southern Florida (Pilsbry 1948), its range is expanding, and it now occurs in central and northern Florida, Louisiana, and Texas (Dundee 1977), and in Mexico (Naranjo-Garcia et al. 2007).

Typically, *L. floridana* is characterized by the presence of a narrow light-colored dorsomedial stripe, and broader, irregular dark dorsolateral stripes. The color pattern is variable, however, especially the dorsolateral stripes, which may be reduced to a series of spots or even absent. Dorsally, it is brownish in color, varying from chocolate to yellowish brown or tan. Consequently, external characters are not reliable for identification, and much of the literature for this genus is questionable (Thomé 1989). Baker (1925), and more recently Gomes (2007), have illustrated the twisted, corkscrew-like form of the penis in *L. floridana*, which is the best morphological indicator of species identity, but too often this character has not been used for identification.

Pilsbry (1948) described *L. floridana* as "voracious", and certainly this large slug appears able to consume a great deal of plant matter. Thus far, it is usually reported only as an occasional pest in Florida, though due to its nocturnal feeding behavior its damage could be overlooked or misidentified. The introduction of *A. cantonensis* to the

mainland USA, and subsequent spread through populations of resident (both indigenous and nonindigenous) molluscs (Campbell & Little 1988; Teem et al. 2013), is perhaps of greater threat to humans, as this and other invasive molluscs often are found in association with humans, who are at risk of being infected. The biology of *L. floridana*, especially the food and habitat associations, are unreported. Thus, we conducted a series of studies on the biology, food suitability, and control of these slugs.

## Materials and Methods

### LIFE HISTORY OBSERVATIONS

Slug collections were made in the Miami and Gainesville areas over a 2-year period and used to establish a breeding colony. They were cultured in plastic boxes measuring 25 × 18 × 10 cm (L × W × D) and partly filled with moist potting soil (Robin Hood garden soil, Hood Landscaping, Adel, Georgia) supplemented with decaying leaves and bark. The mineral content was 3.6% clay, 4.0% silt, and 92.4% sand. The level of organic matter (without the supplemental leaves and bark) was 11.5%. The slugs were fed Romaine lettuce (*Lactuca sativa* L., cv. *longifolia* Lam.; Asteraceae) at 2-3 d intervals and maintained at 26 °C and 14:10 h L:D photoperiod. F2 to F4 progenies were observed for basic life history information, including age (size) at reproduction, growth trends, length of life, egg and hatchling dimensions, length of the egg stage, number of eggs per cluster, and slug burrowing behavior. Slugs were dissected, and the male genitalia examined to confirm identity.

Long-term slug growth and survival patterns were monitored using 4 replicate plastic boxes as described earlier for culture, each containing soil, Romaine lettuce, and 20 newly hatched (1 d old) slugs. At 2-3 d intervals, the slugs were provided with more than enough lettuce to satisfy their appetite. The weights of 20 randomly selected slugs (5 from each replicate box) were determined approximately weekly with a Mettler Toledo A104 analytical balance. The occurrence of egg clusters was recorded, and eggs removed. Length and width measurements of the eggs were made with an ocular micrometer. Eggs were placed on moist paper towels to induce hatching. When the soil became slimy or excessively wet (the slugs would no longer burrow into the soil) the soil was replaced, usually at 4-6 wk intervals. The survival of the slug populations was assessed by counting the surviving slugs at these intervals as well. This study was terminated after 18 mo, when survival fell to below 50% of the initial population. The pattern of growth (weight gain) was modelled with linear and polynomial regression (GraphPad Prism, GraphPad Software, San Diego, California).

The preference of slugs for differing soil moistures was assessed using a gradient of different soil moisture levels. To attain this gradient, 2 of the aforementioned plastic boxes had one end removed and then

the 2 cut ends glued together to form a single long box measuring 49 x 18 x 10 cm (L x W x D). Temporary partitions were placed equidistant in the box to create 7 equally sized spaces, 18 x 7 x 10 cm (L x W x D). Soils with 7 different levels of moisture were inserted sequentially (highest to lowest moisture levels). Prior to oven-drying the soil to a constant (dry) weight and then adding water to create uniform soil moisture levels, the soil was screened to remove any large contaminants such as stones and twigs. A ball mill was used to mix the soil and water thoroughly and uniformly. The moisture levels that we created were based on field capacity (moisture retention capability), and were 100, 83, 67, 50, 33, 17, and 0% of field capacity. Field capacity was determined based on water absorption capability of oven-dried soil, with 100% field capacity being 68 g water/100 g dry soil. At the end of the study, 16 h after creating the moisture gradient and releasing the slugs, soil samples were taken from each section, oven dried, and the change in weight (moisture) was calculated to determine how the moisture gradient retained its integrity.

For these soil moisture studies, soil was added in each section to a depth of 8 cm, leaving about 2 cm of headspace at the top of the box for lettuce and slugs. Then the partitions were removed, lettuce was placed along the entire length of the box, and 21 partly grown (3-6 g) slugs were released, with 3 slugs placed on the surface of each moisture level. A solid cover was placed atop the box and the slugs were allowed to feed overnight and to redistribute themselves. Their distribution in the soil was determined the following morning by digging up each section. There were 4 replicate boxes (84 slugs) in this test. After observing that many of the slugs did not display normal behavior and bury themselves in the soil in the morning, a second study (84 slugs) was conducted using a cover that was vented, which resulted in lower humidity in the boxes, and induced the slugs to bury themselves. The ambient humidity of the headspace above the soil, measured with a Hobo data logger (Onset Computer Corporation, Bourne, Massachusetts) during the dark period when slugs are active, was about 90% for the solid cover but only about 75% for the vented cover. All the slugs in the vented containers displayed normal behavior, burrowing into the soil on the morning following treatment, shortly after the lights turned on. Care was taken to orient the 4 containers in different directions to avoid the possibility of interference with slug behavior by light.

In each of the aforementioned soil moisture tests, the slug distribution data were converted to % of total slugs burrowing into the soil at each moisture level. The data did not meet the assumption of normality according to the D'Agostino and Pearson omnibus normality test (GraphPad Prism). Prior to analysis, % values were transformed to decimal arcsin square root plus 0.5 values to normalize the data. Data were analyzed using one-way ANOVA (GraphPad Prism). Significant differences in slug distribution were identified with the Bonferroni multiple comparison test.

## SUITABILITY OF DIFFERENT FOODS

The principal diet study was designed to assess suitability of different plants using growth of young slugs. Thus, newly hatched slugs were measured for growth and survival on diets of 7 representative ornamental plants, 8 vegetable crop plants, 7 weeds, and 8 other potential foods. Romaine lettuce was used as a standard (control) because these slugs, as well as most terrestrial plant-feeding molluscs, accept it readily. The diets were monitored every 2-3 d and replaced as needed to assure freshness and a good environment for the slugs. The slugs were maintained under the temperature and photoperiod conditions mentioned previously.

Ornamental plant foliage tested was four o'clock, *Mirabilis jalapa* (Nyctaginaceae); Philippine violet, *Barleria cristata* (Acanthaceae);

Persian shield, *Strobilanthes dyeriana* (Acanthaceae); polka dot plant, *Hypoestes phyllostachya* (Acanthaceae); cat's whiskers, *Orthosiphon aristatus* (Lamiaceae); coleus, *Solenostemon scutellarioides* (Lamiaceae); and aluminum plant, *Pilea cadierei* (Urticaceae). Weed foliage evaluated was wild poinsettia (Mexican fireplant), *Poinsettia heterophylla* (Euphorbiaceae); Florida beggarweed, *Desmodium tortuosum* (Fabaceae); Florida pusley, *Richardia scabra* L. (Rubiaceae); Cuban jute, *Sida rhombifolia* (Malvaceae); Benghal dayflower, *Commelina benghalensis* (Commelineaceae); and common purslane, *Portulaca oleraceae* (Portulacaceae). Vegetable crops tested were green bean, *Phaseolus vulgaris* (Fabaceae); sweet corn, *Zea mays* (Poaceae); carrot, *Daucus carota* (Apiaceae); pumpkin, *Curcubita moscata* cv. Seminole; okra, *Abelmoschus esculentus* (Malvaceae); basil, *Ocimum basilicum* (Labiatae); and garden pea, *Pisum sativum* (Fabaceae). All vegetable tissue tested was foliage except for carrot, where the below-ground portion was evaluated. Additionally, other non-foliage materials were tested: excrement of cattle, horses, chickens and grasshoppers, as well as gold-fish granules (Aqueon Products, Franklin, Wisconsin); leaf litter from mixed deciduous trees; paper towels, and white mushroom, *Agaricus bisporus*.

The ornamental plants and basil were procured from home gardens. The other vegetable crops were cultivated under shadehouse conditions at the UF Entomology & Nematology Department except for the carrots, white mushrooms, and Romaine lettuce, which were purchased from a grocery store. The weeds used were gathered from near the Entomology & Nematology Department or home gardens. All plant samples came from areas where no pesticides had been recently used. Young slugs ( $n = 16$  per diet) were placed individually in cylindrical plastic containers (250 mL; 11 cm dia x 4 cm) with paper towels to maintain humidity in each of the diets. We used 480 slugs for the 30 diet treatments. The slugs were weighed weekly with the analytical balance at the start of the study and then weekly for 35 d (long enough for dietary effects to be evident), and mortality was recorded. To assess effects of diet suitability on survival, data on mean slug weight after 35 d on each diet, and mean percent mortality on each diet, were analyzed using the nonparametric Spearman correlation coefficient (GraphPad Prism).

A second diet study was to assess growth on lettuce after feeding different diets. The objective was to determine whether slugs can attain more rapid growth after feeding on less preferred food for 35 d. Thus, after completion of the aforementioned growth studies, any slugs from the diet treatments ( $n = 5-15$  depending on the diet) were transferred to a lettuce diet, and weight recorded after 7 and 14 d. Environmental conditions were as described previously.

## POTENTIAL FOLIAGE CONSUMPTION

To determine potential foliage consumption, leaf consumption by 75 slugs was measured daily for 3 days. Slugs of various weights (0.02-25 g) were used in this assay to assess age (size)-specific consumption. Romaine lettuce was used as the substrate to determine the potential foliage consumption rates because it is readily accepted. Slugs were raised individually on lettuce in 1.75 liter covered plastic containers (18 cm diam, 7 cm high) with a solid, tight-fitting lid and with wet paper towels for 72 h, with consumption measured each 24 h. Environmental conditions were as described previously. The daily foliage consumption was assessed based on weight with the analytical balance, and leaf area with a LI-COR 3000 leaf area meter (LI-COR, Lincoln, Nebraska), respectively. Because the foliage presented to slugs can gain or lose water during the experiment, we established 15 control (lacking slugs) containers to make corrections to the data collected. The weight change in Romaine lettuce in the control containers was determined



by subtracting the initial weight from the final weight, then calculating the mean % change. The mean weight gain in the control containers was subtracted from corresponding weight values in containers being evaluated. In contrast, mean weight loss in the controls was added to corresponding values in the test containers. Thus, the potential foliage consumption values were determined using the adjusted values, though the weight changes among control foliage were minor. Leaf area and weight consumption (225 observations) were graphed against the weight of the slugs. Linear and polynomial regression equations were assessed with Microsoft Excel, and  $R^2$  values were used to estimate the best fit. Relative consumption ( $\text{cm}^2$  or g foliage/g slug/d) was estimated by plotting the leaf consumption values along the regression line against slug weight, and fitted in the aforementioned manner. The relationship between leaf weight loss and leaf area consumption was also determined with a linear regression equation.

Slugs usually feed on mixed diets. Thus, although many of the plants tested for suitability by young slugs were found to be suboptimal, this does not preclude slugs from eating these plants occasionally, and perhaps causing damage. Defoliation potential of selected plants by slugs was assessed by providing hungry slugs (following 48 h without food) with some of the plant species previously fed to small slugs, plus some plants not tested with young slugs. Five 3–4 g slugs were individually tested with each plant species. The test vegetation and slugs were maintained in 500 mL (11 cm dia x 7 cm) cylindrical plastic containers with wet paper towels to maintain humidity. The leaf area was determined prior to introduction of the slugs, and then again after 24 h, with the difference constituting consumption. We used a 24 h period because we were interested only in acceptance of different plants by hungry slugs, and were not interested in tabulating long term rates of consumption. Two leaves of each plant served as controls to determine if leaf area changed due to moisture loss or uptake during the trial. Leaf consumption was determined with the leaf area meter. The plants evaluated that also were tested previously for suitability by young slugs were four o'clock, Philippine violet, polka dot plant, cat's whiskers, aluminum plant, coleus, wild poinsettia, and green bean. Novel plants tested with the larger slugs were hibiscus, *Hibiscus rosa-sinensis* (Malvaceae); firespike, *Odontonema strictum* (Acanthaceae); peregrina, *Jatropha integerrima* (Euphorbiaceae); marigold, *Tagetes patula* (Asteraceae); Madagascar periwinkle (also known as vinca), *Catharanthus roseus* (Apocynaceae); New Guinea impatiens, *Impatiens hawkeri* (Balsaminaceae); zinnia, *Zinnia* sp. (Asteraceae); begonia, *Begonia* sp. (Begoniaceae); dwarf oyster plant, *Tradescantia spathacae* (Commelinaceae); chrysanthemum, *Chrysanthemum* sp. (Asteraceae); American burnweed, *Erechtites hieraciifolia* (Asteraceae); blanketflower, *Gaillardia* sp. (Asteraceae); sunflower, *Helianthus* sp. (Asteraceae), and daylily, *Hemerocallis* sp. (Zanthorrhoeaceae).

## EVALUATION OF MOLLUSCICIDE BAITS

We evaluated 4 commercially available molluscicide baits, each containing a different toxicant, for effectiveness against *L. floridana* in laboratory tests. The baits tested were Corry's Slug and Snail Pellets, containing 3.25% metaldehyde (Matson LLC, North Bend, Washington); Ecosense Slug and Snail Killer, containing 1% iron phosphate (Ortho, Marysville, Ohio); Ferro Slug and Snail Bait, containing 5% sodium ferric EDTA (Neudorff North America, Emmertal, Germany); and Niban Granular Bait, containing 5% orthoboric acid (Nisus Corporation, Rockford, Tennessee). An untreated (no bait) treatment was also included as a control. We tabulated mortality and lettuce consumption daily for 6 d post-treatment, then at 2 d intervals until day 12. Mortality was assessed by prodding the slugs with a spatula, and they were determined to be dead if they did not respond and their integument was

discolored or disintegrating. Lettuce consumption was determined by weight loss (weight before exposure to slugs minus weight after exposure), using the analytical balance. The baits were tested by confining slugs to a 1.75 liter cylindrical plastic container (18 cm dia x 7 cm) with a solid, tight-fitting lid. The containers contained about 2 cm of moist soil in the bottom, a Romaine lettuce leaf, 0.5 g of bait, and 5 slugs of uniform size (4–5 g each, about 5 months old). The bait was scattered over the soil surface, where it quickly absorbed moisture. There were 5 replicate containers for each treatment, using a total of 125 slugs.

The cumulative mortality and daily lettuce consumption data were subjected to 2-way repeated measure ANOVA using GraphPad Prism with molluscicide type and time (days post-treatment) as the principle variables. Means were separated with the Bonferroni multiple comparison test. For lettuce consumption on days 6–12, the total consumption in each 2 d interval was divided in half to estimate daily consumption. The mortality data were transformed to decimal arcsin square root plus 0.5 values prior to analysis, but the consumption data did not require transformation because the data were normally distributed according to the D'Agostino and Pearson omnibus normality test (GraphPad Prism).

The failure of orthoboric acid (Niban) to induce mortality or to reduce feeding by slugs caused us to look more closely at toxicity of orthoboric acid, the active ingredient in Niban. Previously we determined that Niban was toxic to the Cuban brown snail, *Zachrysia provisoria* (Pfeiffer, 1858), and although it was slow-acting as a toxicant, it rapidly reduced plant feeding even in the absence of mortality (Capinera 2013). Thus, we hypothesized that the slugs did not feed on the Niban bait, and conducted an experiment to assess indirectly the cause of the failure. To assess the toxicity of orthoboric acid, we mixed 2 concentrations (5%, 10%) of orthoboric acid (boric acid, Fisher Scientific, Fair Lawn, New Jersey) in water and sprayed it on the adaxial surface of lettuce leaves until run-off. After allowing for drying, one leaf with each foliage treatment was placed in each of 4 cylindrical plastic containers (1.75 L; 18 cm dia x 7 cm) with a moistened paper towel, and 5 slugs (3–7 g each) were added to each container with 0% (water-only check), 5%, and 10% orthoboric acid-treated foliage. They were maintained at 26°C and monitored at 2 d intervals for 8 d. Percent mortality data were transformed (decimal arcsin square root plus 0.5) and subjected to a repeated measures 2-way ANOVA (molluscicide and days post treatment). Significant differences in mortality were identified with the Bonferroni multiple comparison test (GraphPad Prism).

Because there is a report of neem oil serving as a feeding stimulant for the snail *Zonitoides arboreus* (Say) (Hollingsworth & Armstrong 2003), we also examined the feeding of *L. floridana* slugs on orthoboric acid (Niban) bait or lettuce foliage that had been treated with neem oil (Triple Action Neem Oil, Southern Ag, Palmetto, Florida). For this orthoboric acid bait test, we mixed 0, 0.5, and 4.0% neem oil (in water) with orthoboric acid bait at the concentration of 10 ml neem solution in 40 g bait, and administered the bait to slugs in the aforementioned manner of bait assessment. Lettuce consumption and mortality were monitored daily for 7 days. Data were data analyzed in the aforementioned manner.

Comparative feeding response of slugs for neem-treated or untreated (water only) foliage was assessed using lettuce leaf discs. Leaf discs were 2 cm dia and punched from fresh lettuce leaf tissue immediately before application of test solutions. Neem was administered to the adaxial surface of lettuce discs at 3 concentrations (0, 0.8, 3.2%) and allowed to dry. Leaf discs were used because this was a short-term test and not much foliage was needed, and because in a choice test equal amounts of foliage are imperative. The discs and slugs then were confined to cylindrical plastic containers (500 mL; 11 cm dia x 7 cm) with moist paper toweling in the bottom to avoid early drying of leaf

material. Each neem-treated disc was paired with a water-treated disc, and the relative proportions of each disc consumed by a single slug in a 24 h period determined with the leaf area meter. There were 20 replicate tests for each pair of neem concentrations; data from the small number of slug tests where no consumption occurred were deleted. Leaf consumption data were converted to decimal arcsin square root plus 0.5 prior to analysis with a paired t-test (GraphPad Prism).

## Results

### LIFE HISTORY OBSERVATIONS

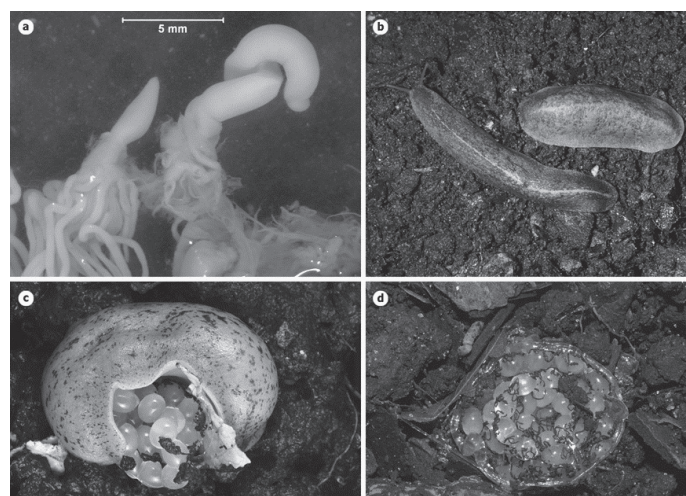
Slug identity was confirmed by dissection of the male genitalia (Fig. 1a). The penis is contained within a sheath or pouch-like structure that must be cut open to observe the diagnostic features. The body size and color patterns were quite variable, even among slugs of the same age (Fig. 1b), so examination of the genitalia is critical.

Under laboratory conditions, most egg production resulted from slugs of intermediate age and size (approximately 150-350 days after hatch, 3-7 g in weight), though some eggs were produced by older slugs. Eggs were deposited in clusters, either in air pockets within the soil, or on the soil surface. The ovipositing slug wrapped itself around the egg cluster while depositing the eggs (Fig. 1c), with the act of oviposition often requiring 2 or more days for completion of the egg cluster. The eggs in each cluster were initially deposited loosely, but the latter eggs were contained in a transparent sheath (the 'egg string' of Rueda 1989), and deposited in concentric circles around the outside of the cluster. Strands of dark material ('feces' of Rueda 1989), which appeared to be fecal matter but were much drier and thinner than typical fecal matter, were deposited on the surface of the cluster (Fig. 1d). The number of eggs in 24 clusters averaged  $45.7 \pm 19.6$  (SD) eggs, with a range of 6-78 eggs. This mean value may be an underestimate, however, because smaller clusters sometimes lacked the final wrapping of eggs and dark stringy deposits, perhaps suggesting that slug oviposition was interrupted. The eggs were oval, and when measured ( $n = 30$ ) with an ocular micrometer, averaged  $7.4 \text{ mm} \pm 1.1$  (SD) in length (range 6.0-9.8 mm) and  $4.8 \text{ mm} \pm 0.4$  (SD) in width (range 4.0-5.5). The eggs initially were clear, but became clouded with time, and acquired an orange-brown tint as they matured. Eggs hatched in about 2 weeks when cultured at 26 °C. Perhaps reflecting the protracted oviposition

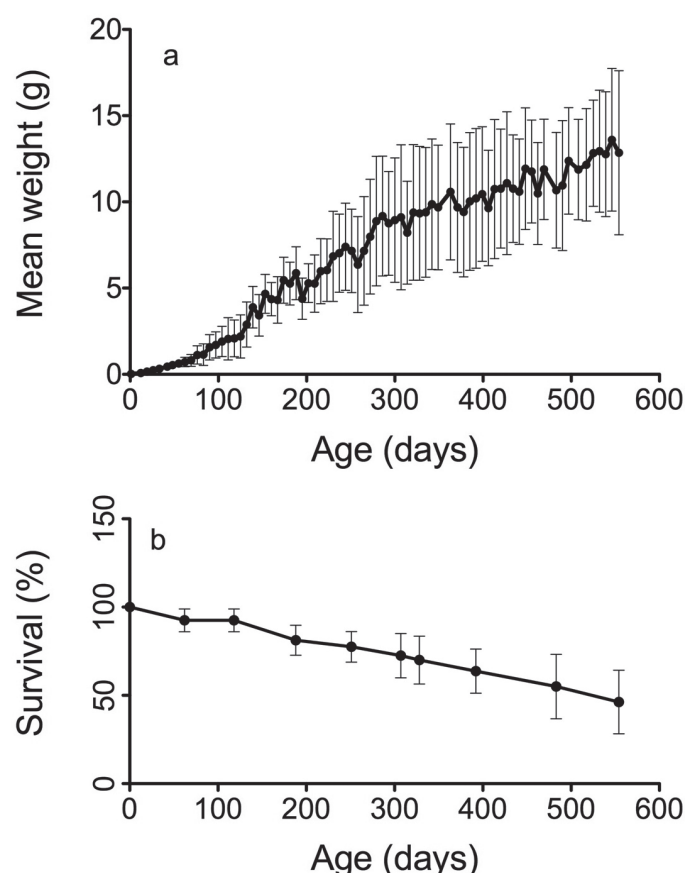
period, hatching was not synchronous, usually requiring 3-4 days for all the eggs to hatch from a single cluster. The proportion of eggs that hatched successfully was highly variable (0-100%), and often a small proportion of eggs hatched, though this may be an artifact of artificial culture conditions.

Hatchlings initially were pale, almost colorless, but within a day they acquired light brown coloration and then developed a darker brown dorsal stripe running the length of the body, and covering about one third of the width of the body. The dorsolateral regions gradually became darker until the dark dorsal stripe was no longer evident. Their initial (contracted) size was 2-3 mm wide and 4-7 mm long. After attaining a length of 15-20 mm, a thin light dorsal stripe typically began to appear, and usually remained evident throughout the life of the slug. However, in exceptionally light- or dark-colored individuals the light dorsal stripe was sometimes absent.

About half of the slugs survived for 18 months, which is consistent with the known life spans of other veronicellids (usually 2 years) and other terrestrial slugs (usually given as 2-5 years) (Heller 1990). They became quite large, attaining a maximum mean live weight of about  $13.6 \text{ g} \pm 4.1$ (SD) with a range of 6.0-24.9 g after about 18 months (Fig. 2), though on occasion we have produced individuals up to 28.5 g and measuring (contracted) 10 cm in length and 3 cm in width. A high degree of variability in size was apparent throughout most of the slug development period. After 18 months some slugs were up to 4 times as large as other slugs. The pattern of growth was nearly linear ( $-0.029 + 0.025x$ ;  $R^2 = 0.680$ ;  $P < 0.0001$ ) until 18 months of age; the fit of a nonlinear line (second order polynomial) improved the fit only marginally ( $R^2 = 0.690$ ).



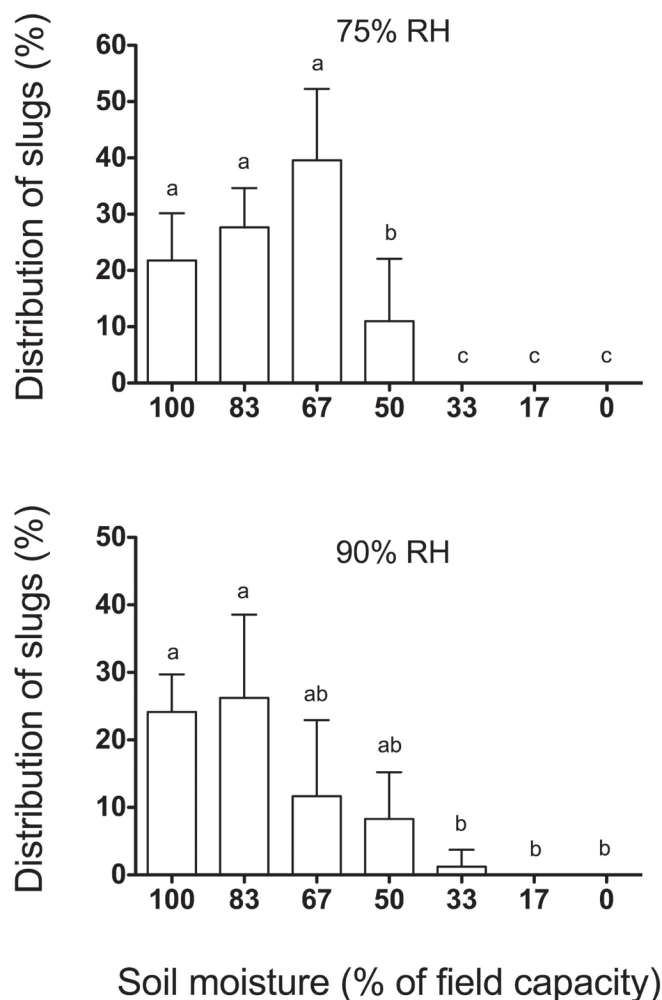
**Fig. 1.** *Leidyula floridana*: (a) dissected male genitalia, showing exsheathed penial gland (left) and penis (right); (b) adults, showing extended form (left) and contracted form (right); (c) adult depositing eggs; (d) completed egg clutch.



**Fig. 2.** *Leidyula floridana*: (a) growth (change in mean wet weight) and (b) survival over an 18 month period under laboratory conditions. Error bars indicate SD.

The soil moisture apparatus was substantially successful in providing the desired separation of moisture levels for moisture preference tests. Most levels lost very little moisture. The 100% soil capacity soil samples lost the most, 16% in the unvented container and 27% in the vented container. In the other soil moisture levels, moisture retention averaged 97% in the unvented container and 94% in the vented container.

The slugs in the vented containers (75% RH) behaved normally, burrowing into the soil soon after 'daybreak' (lights-on). Their distribution was significantly affected by soil moisture ( $F = 27.27$ ;  $df = 6, 21$ ;  $P < 0.0001$ ). Most of the slugs were found in the higher soil moisture levels (Fig. 3a) though the slugs did not discriminate among the treatment regimes of 67, 83, and 100% of soil capacity. The 50% soil capacity had significantly fewer slugs than the higher moisture levels, and significantly more than the lower moisture levels. The unvented (90% RH) container had fewer slugs burrowing into the soil, but the distribution of slugs that burrowed were found significantly ( $F = 11.72$ ;  $df = 6, 21$ ;  $P < 0.0001$ ) more frequently in the higher soil moisture levels. In this unvented container study, however, both the 67 and 50% soil moisture treatments had intermediate numbers of slugs burrowing into the soil (Fig. 3b). In long-term growth and survival studies, the slugs displayed the same behavior, tending to seek shelter in the soil or beneath bark chips during the daylight hours.



**Fig. 3.** Mean distribution of burrowing slugs in relation to soil moisture levels after release into vented (75% RH) and unvented (90% RH) cages. Error bars indicate SD. Bars topped by the same letter are not significantly different according to the Bonferroni multiple comparison test.

## HOST PLANTS

Among the crop plants tested, Romaine lettuce was superior for young slug weight gain (Fig. 4a). Slugs fed on lettuce increased about 10-fold in weight over the 35 d period of evaluation, whereas slugs fed on Seminole pumpkin, okra, and green bean foliage displayed about 300% increase in weight. Slugs also fed on basil, carrot, pea, and sweet corn; however, their weight remained nearly constant during the study.

The ornamental plants that were evaluated seemed less suitable as hosts for young slugs. Slugs gained some weight, approximately doubling in weight when feeding on polka dot plant, 4 o'clock, coleus, and cat's whiskers (Fig. 4b). They also fed on Persian shield, aluminum plant, and Philippine violet, initially gaining some weight at the first week, then decreasing in weight over 35 days. Although they did not prosper on these latter plants, most survived the 35-day duration of the study.

Among the weeds tested, Florida pusley (*Richardia scabra* L.; Rubiaceae) and wild poinsettia (*Euphorbia cyathophora* Murray; Euphorbiaceae) were suitable host plants for young slugs, allowing them to gain about 700% in weight during the test (Fig. 4c). Cuban jute, Old World diamond flower, and Florida beggarweed were less suitable host plants, though the slugs gained about 300-400% in weight. Slugs maintained constant weight when they were feeding on common purslane. Slugs survived only 2 weeks when feeding on Benghal dayflower.

The slugs died within a week when feeding on goldfish granules, chicken feces, and grasshopper feces. Cattle and horse feces, leaf litter, white mushroom, and paper towels were only slightly suitable for the growth of young slugs over the 35 days of assay (Fig. 4d). Nevertheless, the slugs survived when feeding on cattle feces and leaf litter, and when moved to lettuce, they commenced growth (Fig. 5). A very consistent pattern of growth stimulation was evident for most diets, including the less suitable plant hosts, once the slugs gained access to more suitable food (lettuce). The mean weight increase was 82% by day 14.

Weight gain was a suitable index of plant suitability, as judged by slug survival. Weight gain by young slugs and % mortality were significantly negatively correlated (Spearman  $r = -0.531$ ;  $P = 0.007$ ). Mortality was quite variable among the different diets (Fig. 6).

## POTENTIAL FOLIAGE CONSUMPTION

Leaf area consumption ( $\text{cm}^2$ ) was adequately estimated from leaf weight loss (g) by a linear regression equation:  $y = 0.5775 + 34.383x$ ;  $r^2 = 0.919$ . This allows interconversion of these 2 metrics, and we present both on the consumption graphs.

For smaller slugs, leaf area consumption increased with size. However, if slug weight exceeded about 8 g, consumption started to drop (Fig. 7a), indicating a declining consumption rate over time. The pattern of consumption can be described by a second order polynomial equation ( $y = -0.1371x^2 + 2.3678x + 4.1128$ ;  $R^2 = 0.178$ ). The mean peak consumption was about  $15 \text{ cm}^2$  or  $0.410 \text{ g/d}$ . However, some individuals consumed over  $40 \text{ cm}^2$  or  $1.5 \text{ g/d}$ . The young slugs consumed relatively more foliage ( $\text{cm}^2$  or  $\text{g foliage/g slug/d}$ ) than the old ones, so the relative consumption rate decreased with age (Fig. 7b). The second order regression equation describing the relative consumption relationship by young slugs is  $y = 0.0061x^2 - 0.0952x + 0.4101$ ;  $R^2 = 0.974$ .

When several prospective host plants were assessed for consumption using larger (3-4 g) slugs, the results were quite variable. Leaf area consumption (mean  $\text{cm}^2 \pm \text{SD}$ , maximum) for each plant species tested was: four o'clock,  $8.2 \pm 8.4$ , 22.6; Philippine violet,  $1.3 \pm 1.1$ , 3.0; polka dot plant,  $6.5 \pm 5.0$ , 11.7; cat's whiskers,  $1.4 \pm 2.9$ , 6.7; aluminum plant, 0; coleus,  $2.7 \pm 1.6$ , 4.1; wild poinsettia,  $14.7 \pm 4.5$ , 36.4; green bean,  $2.5 \pm 2.3$ , 6.0; hibiscus,  $0.1 \pm 0.3$ , 0.6; firespike,  $1.6 \pm 1.1$ , 2.6; peregrina, 0; marigold,  $2.5 \pm 1.9$ , 4.9; Madagascar periwinkle,  $0.7 \pm 1.4$ , 3.2;



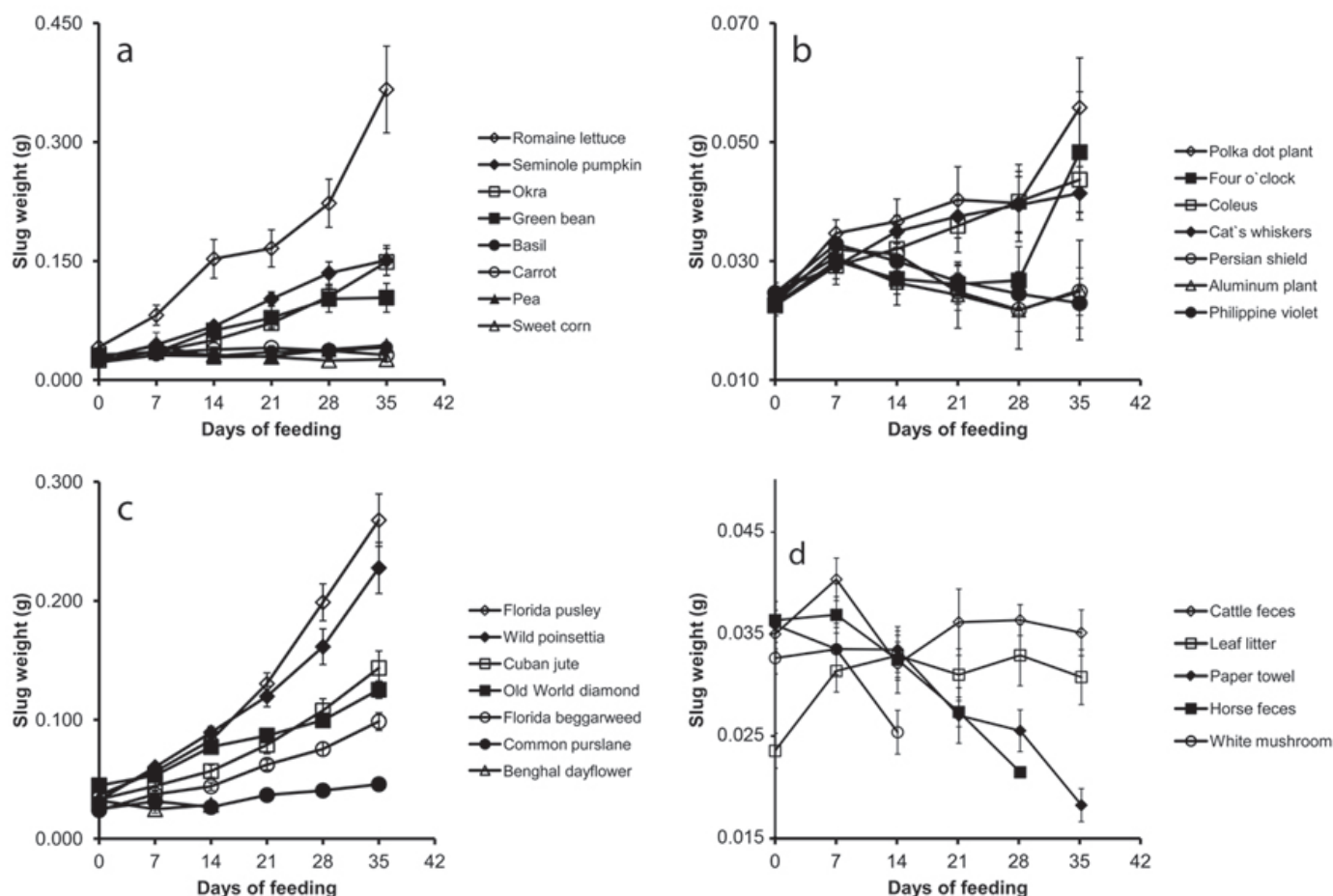


Fig. 4. Growth (mean change in wet weight) of young *L. floridana* during the first 6 weeks of life when provided with different potential food resources: (a) vegetable plants; (b) ornamental plants; (c) weeds; (d) other materials. Error bars indicate SD.

New Guinea impatiens,  $1.0 \pm 1.2$ , 2.8; zinnia,  $7.9 \pm 2.3$ , 10.1; begonia, 0; dwarf oyster plant,  $3.1 \pm 4.2$ , 10.0; chrysanthemum,  $3.2 \pm 2.6$ , 7.3; American burnweed,  $10.2 \pm 8.0$ , 21.7; blanketflower,  $4.6 \pm 2.3$ , 7.7; sunflower,  $6.7 \pm 6.6$ , 17.0; daylily,  $0.4 \pm 0.4$ , 1.1.

#### EVALUATION OF MOLLUSCICIDE BAITS

Molluscicide baits induced significantly different levels of slug mortality ( $F = 103.47$ ;  $df = 4,20$ ;  $P < 0.0001$ ). The effect of the molluscicide was dependent on time ( $F = 106.70$ ;  $df = 8,160$ ;  $P < 0.0001$ ), and the molluscicide-time interaction was significant ( $F = 26.22$ ;  $df = 32,160$ ;  $P < 0.0001$ ). The metaldehyde-containing bait (Corry's) provided significant control beginning 1 d post-treatment, but the iron phosphate (Ecosense) and sodium ferric EDTA (Ferrox) did not induce significantly elevated mortality until 4 days post-treatment (Fig. 8a). Mortality in the metaldehyde treatment remained higher than in the iron-based treatments for the 12 d of the study. The orthoboric acid-based bait (Niban) did not induce mortality during the duration of the study.

Foliage consumption also was significantly affected by the bait treatments ( $F = 129.67$ ;  $df = 4,20$ ;  $P < 0.0001$ ). The effect of the molluscicide was dependent on time ( $F = 24.79$ ;  $df = 8,160$ ;  $P < 0.0001$ ), and the consumption-time interaction was significant ( $F = 3.34$ ;  $df = 32,160$ ;  $P < 0.0001$ ). Despite the failure of Ecosense and Ferrox to induce mortality early in the study, they significantly reduced lettuce foliage consumption throughout the study (Fig. 8b). The reductions in foliage consumption in the iron-based treatments (Ecosense, Ferrox) were not significantly different from the level in the metaldehyde

treatment (Corry's). The orthoboric acid treatment (Niban) did not reduce consumption relative to the control.

When a liquid application of orthoboric acid was applied to lettuce foliage, the results were different: orthoboric acid induced mortality. In this study, the molluscicide effects were significant ( $F = 24.42$ ;  $df = 2,9$ ;  $P = 0.0002$ ), the effect of the molluscicide was dependent on time ( $F = 32.70$ ;  $df = 3,27$ ;  $P < 0.0001$ ), and the interaction was significant ( $F = 7.39$ ;  $df = 6,27$ ;  $P < 0.0001$ ). Neither rate of orthoboric acid application induced significant mortality, relative to the control, at 2 d post-treatment. However, at 4 d post-treatment the mean mortality in the 5 and 10% orthoboric acid treatments were 35 and 45%, respectively, significantly ( $P < 0.05$ ) higher than the 0% mortality in the control. At 6 d post-treatment, the results were similar: the mean mortality in the 5 and 10% orthoboric acid treatments were 65 and 90%, respectively, significantly ( $P < 0.001$ ) higher than the 0% mortality in the control. At 8 d post-treatment, the mean mortality in the 5 and 10% orthoboric acid treatments were 80 and 90%, respectively, significantly ( $P < 0.001$ ) higher than the 5% mortality in the control.

Application of neem oil to the orthoboric acid (Niban) bait did not significantly affect lettuce leaf consumption. The amended orthoboric acid molluscicide treatment was not significant when tested by 2-way ANOVA ( $F = 1.72$ ;  $df = 2,63$ ;  $P = 0.188$ ). The molluscicide-time interaction ( $F = 0.22$ ;  $df = 12,63$ ;  $P = 0.997$ ) also was not significant. However, there was a significant time (day) effect ( $F = 4.21$ ;  $df = 6,63$ ;  $P = 0.001$ ). This latter data signifies only that consumption varied among days. No mortality occurred during the 7 d test period. Similarly, slugs did not



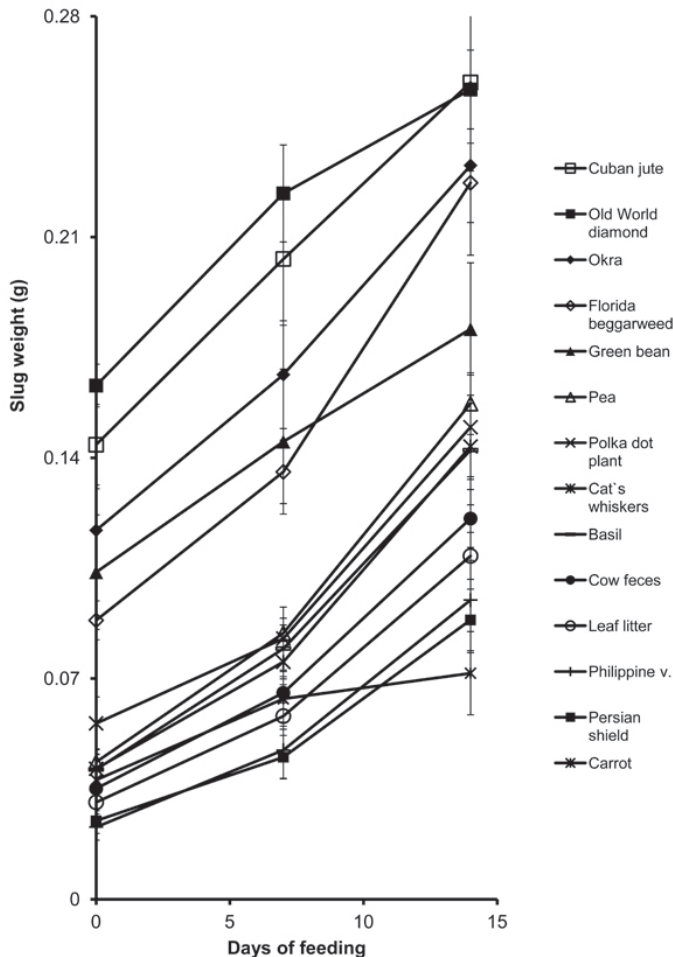


Fig. 5. Growth (mean change in wet weights) of young *L. floridana* after transfer to a Romaine lettuce diet from less suitable hosts. Error bars indicate SD.

discriminate between neem-treated and untreated lettuce foliage in choice tests ( $t = 0.504$ ;  $df = 13$ ;  $P = 0.622$  for the 0.8% neem, and  $t = 0.375$ ;  $df = 19$ ;  $P = 0.711$  for the 3.2% neem).

## Discussion

### LIFE HISTORY OBSERVATIONS

South (1992) noted that there was not a great deal of information about veronicellid slug biology, and with the possible exception of their taxonomy (Thomé 1989; Maceira 2003; Gomes & Thomé 2004), our knowledge about them has not much improved since that assessment. The biology and control of the species known from Central America are summarized by Rueda et al. (2002). Rueda (1989) also conducted research in Florida, reportedly with *Sarasinula plebeia* (Fischer, 1868), but this species is not known from Florida so it is possible that this research involved the similar-appearing *L. floridana*. The laboratory studies by Rueda (1989), conducted with slugs originally collected from Homestead, Florida, produced results that were both similar to, and different from, the results reported here. Rueda's slugs developed faster, attaining a mean weight of 15.3 g in 138 d, then declined to 10.6 g by 390 d. Rueda's slugs began oviposition at 134 d and produced egg clutches of 30-52 eggs. Thus, in comparing the Rueda (1989) studies with the data reported here, the time to initiation of egg deposition and

mean number of eggs per clutch are not markedly different. In contrast, the longevity of slugs was greater in our study, and the mean weight continued to increase for a longer period of time. In fact, the linearity of the growth pattern suggests that the maximum weight was not attained even after 18 mo (554 d). The suitability of bean foliage and the unsuitability of carrot were consistent in both studies. Oviposition behavior also was similar in both studies, though most veronicellids have similar oviposition behavior.

Lacking the protective shell of their snail relatives, slugs normally are associated with moist conditions. However, the *L. floridana* slugs displayed broad tolerance to soil moisture conditions. Though clearly orienting to high moisture levels, their tolerance of moderately dry soil conditions (as low as 50% soil moisture capacity) suggests a high degree of robustness. Although slugs commonly are associated with moist conditions, they do not always gravitate to more moist substrates. For example, Getz (1959) compared the orientation of 3 species to a moisture gradient, and found that although *Arion circumscriptus* Johnston, 1828 favored high moisture, *Deroceras reticulatum* (Müller, 1774) and *Deroceras laeve* (Müller, 1774) did not. On the other hand, Young & Port (1991) found that *D. laeve* travelled greater distances, and foraged for longer periods of time, when the soil surface was wet. Similarly, Speiser & Hochstrasser (1998) reported more feeding damage by *Arion lusitanicus* Mabille, 1868 to lettuce when plants were watered in the evening than when watered in the morning.

The inconsistent egg viability of the slug colony was surprising, as the slugs were always cultured in groups, so fertilization should not have been an issue. Willis et al. (2008) reported variable egg viability in *D. reticulatum*, with both soil moisture levels and temperature affecting egg hatch. The optimal conditions for *L. floridana* incubation and hatch have not been determined.

### HOST PLANTS

A few plants allowed rapid growth of young slugs, namely Romaine lettuce, Florida pusley and wild poinsettia. Some vegetable crops (Seminole pumpkin, okra, and green bean) and weeds (Cuban jute, Old World diamond flower, and Florida beggarweed) allowed a 3 to 4-fold increase in weight, so they can be considered to be of intermediate value for growth of young slugs. This suggests that the presence of weeds might favor the occurrence of *L. floridana*, not an unusual situation for plant pests, as they often accept weeds as well as crops (Duval 1971; Chatfield 1976). Interestingly, *Z. provisoria* grew rapidly on certain weeds, especially wild poinsettia (Capinera 2013), which also were suitable for *L. floridana*. *L. floridana* is reported to damage vegetable crops, including potatoes, beans, and tomatoes (Naranjo-Garcia et al. 2007).

Several ornamental plants allowed weight gain of slugs, but it was only marginal growth. However, even if they were not growing, the slugs could survive on several ornamental and other plants, and even a few other substrates such as leaf detritus, for over 30 d. Thus, these less suitable materials may serve to bridge the period between hatch and when more suitable plants are available. Importantly, slugs displaying poor growth can shift to rapid growth once more suitable host material is available. Slugs are known for their resilience and plasticity with respect to food quality (Rollo & Shibata 1991).

In some cases, the slugs performing poorly did not eat each much plant material, but in the case of Florida beggarweed and Old World diamond flower, the slugs fed more vigorously than might be expected given their rate of weight gain on these plants. Allelochemicals commonly deter animals from feeding on plants, but based on the level of

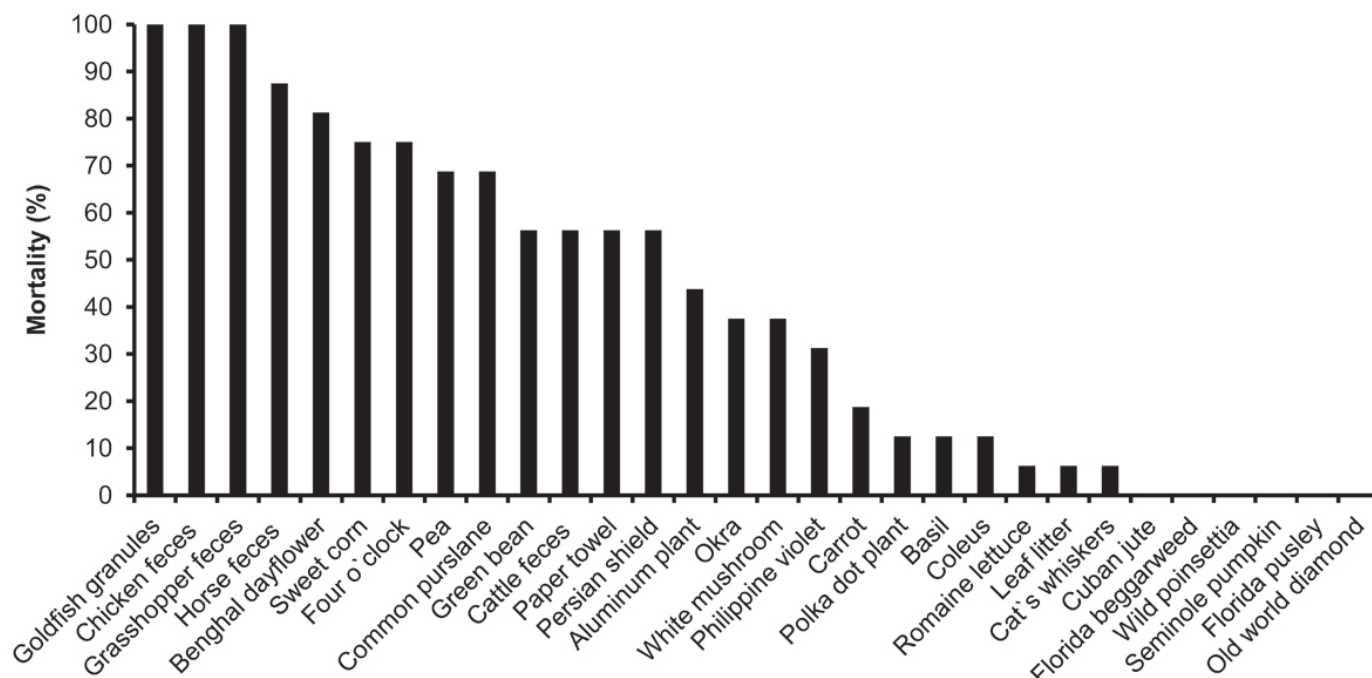


Fig. 6. Total % mortality of newly hatched slugs after being confined to only one diet for 35 d.

feeding, these plants did not contain effective feeding deterrents. Slugs are often quite tolerant of alkaloids and other secondary metabolites (Aguar & Wink 2005). Thus, the relatively poor growth of the slugs feeding on these plants may be related to low nutritional quality of their food.

*Leidyula floridana* displayed considerable differences in feeding and growth when provided with different diets. Although terrestrial molluscs are polyphagous, their acceptance of plants and the suitability of such plants in enhancing and maintaining slug condition can differ depending on the plant species, with slugs avoiding many potential food resources. Particular plant families, plant age, chemical constituents, growth forms, life cycles, and even plant culture methods will influence mollusc feeding, and the feeding behavior differs among mollusc species (Mølgaard 1986; Briner & Frank 1998; Keller et al. 1999; Pérez-Harguindeguy et al. 2003; Holland et al. 2007). Sometimes consistent patterns emerge. For example, the vegetable crop plants attacked by *Arion lusitanicus* in Poland (Kozłowski 2005) tended to be the same as those suitable for *L. floridana* growth in these studies. Information about plant acceptance and suitability is useful in determining sources and harborage of pest species, and for manipulating their populations by attracting them away from valuable or susceptible crops. For example, Raut & Ghose (1983) showed that damage to crop plants by *L. fulica* could be reduced by 33–77% through introduction of non-crop plants.

An important observation was the ability of these slugs to survive for long periods of time on substandard food, and then to grow rapidly when accessing more suitable host plants. The ability of the slugs to survive on diverse organic matter such as leaf litter and weeds suggests that it would be difficult to control these animals completely using cultural practices like clean cultivation.

#### POTENTIAL FOLIAGE CONSUMPTION

The pattern of Romaine foliage consumption by *L. floridana* slugs was similar to *Z. provisorio* snails, with a nonlinear relationship between consumption and mollusc weight (age) (Capinera

2013). In both cases, consumption increased until the molluscs attained a weight of about 7–8 g, then decreased. The pattern of consumption by slugs shown in Fig. 7a represents all data, including a large number of zero values because the slugs did not eat every day. This introduces a high level of variability into the assessment of consumption, which might best be handled by elimination of the zero values. If this is done, the polynomial equation becomes  $y = -0.0392x^2 + 6.0027x + 1.719$ ;  $R^2 = 0.525$ . When the zero values are eliminated, the mean peak consumption estimate is somewhat enlarged, to about 20 cm<sup>2</sup>, or 0.5 g/d. The determination of what estimate of consumption to use is related to the question asked. If the question is 'what is the average consumption', then the equation including the zero values is appropriate. However, if the question is phrased as to address potential meal size, then the zero-free equation might be more appropriate. The relative consumption rate declined as the slugs aged, falling from about 20 cm<sup>2</sup>/g of slug per day when small, to about 0.25 cm<sup>2</sup>/g/d when the slugs weighed about 8 g. This is a similar, but steeper, age-related decline in foliage consumption as compared to *Z. provisorio* (Capinera 2013). Davidson (1976) also reported juvenile *Limax flavus* (Linnaeus, 1758) slugs to have higher ingestion rates than adult slugs.

Larger slugs consumed measurable quantities of foliage in about 80% of the plant species tested. Although the slugs did not consume as much of these plants as they did when using Romaine lettuce as a food source, prospective hosts such as 4 o'clock, polka dot plant, zinnia, blanketflower and sunflower were readily consumed and could be expected to be significantly damaged under field conditions if they are grown in habitats infested with these slugs. Even less readily consumed plants could be damaged if slugs were abundant. Not surprisingly, when the rates of consumption of plants previously tested for suitability for young slugs were compared to foliage consumption by larger slugs, the plant species readily consumed were also species that supported growth in young slugs. Thus, their feeding behavior remains relatively consistent. One pattern that seems to emerge from the feeding trials is ready acceptance of plants in the family Asteraceae.

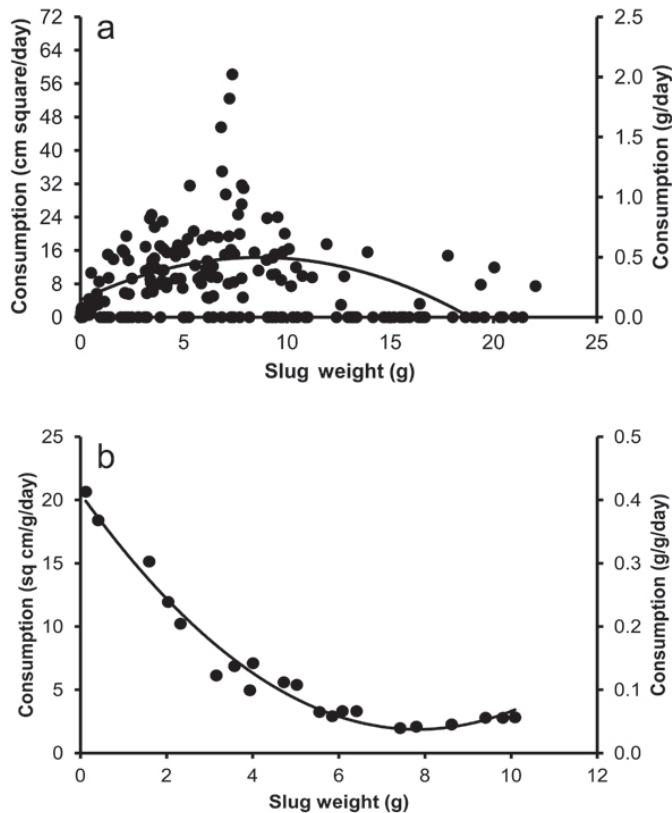


Fig. 7. Foliage consumption (mean leaf area and mean wet weight) patterns by *L. floridana* in relation to mean slug wet weight (age): (a) daily consumption; (b) relative consumption (consumption adjusted for slug weight).

## MOLLUSCICIDE BAITS

The metaldehyde and iron-based molluscicides provided good control of slugs in laboratory trials and reduced foliage consumption, with the metaldehyde product (Corry's) working more quickly. It is important to note that slugs provided with the iron-based bait products displayed reduced foliage consumption almost immediately, despite their continued survival. It might be tempting to conclude that these products are ineffective if slug survival rather than foliage protection is assessed, but foliage protection is usually the ultimate goal of bait applications, and the iron-based bait products greatly inhibited plant consumption. These results are consistent with similar trials using *Z. provisorio* and these same baits (Capinera 2013). Metaldehyde (Corry's) and iron phosphate (Ecosense) baits are well documented to provide control of terrestrial molluscs (Speiser & Kistler 2002; Nash et al. 2007). Sodium ferric EDTA (Ferrox) and orthoboric acid (Niban) are less well studied, though they have been assessed for control of *Z. provisorio* (Capinera 2013) and giant African snail, *Lissachatina fulica* (Bowdich, 1822) (Smith et al. 2013). However, in these *L. floridana* studies the orthoboric acid-based bait was ineffective, a very different response than the aforementioned snail trials. We showed that orthoboric acid is toxic to slugs when it is applied to foliage, so deduce that the bait formulation is not attractive to the slugs, thereby limiting the effectiveness of the potential toxicant. Both *Z. provisorio* and *L. fulica* have broader ranges of acceptable diet elements than does *L. floridana*. For example, in artificial diet trials, *Z. provisorio* consumed 5 synthetic insect diets, whereas *L. floridana* accepted none (Capinera

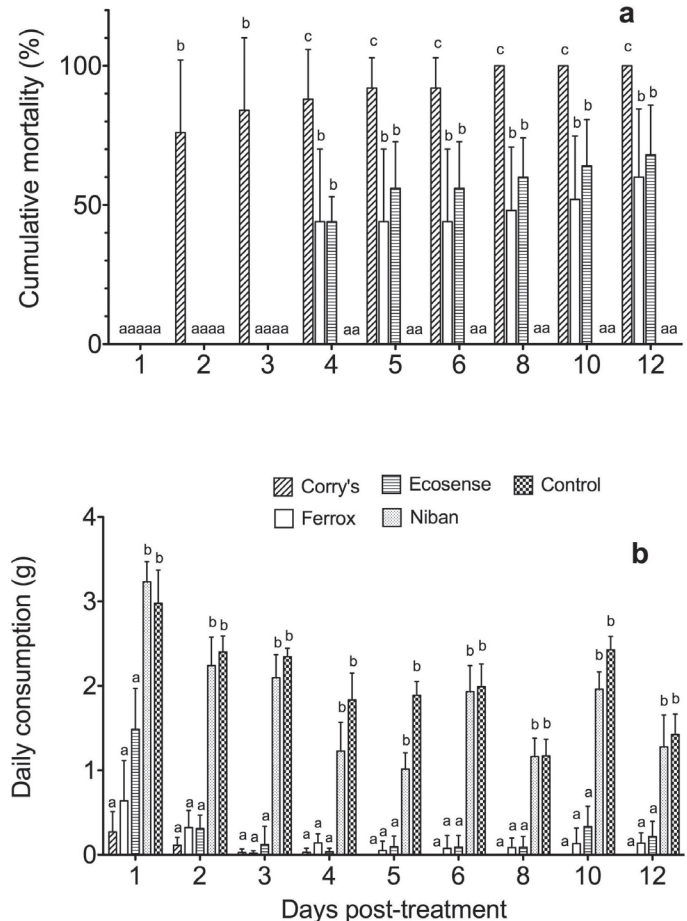


Fig. 8. Effects of different bait treatments on *L. floridana* slugs in relation to time: (a) mean cumulative mortality; (b) mean daily lettuce consumption. Error bars indicate SD. Bars within a date topped by the same letter are not significantly different according to the Bonferroni multiple comparison test.

2012). Despite the report that neem oil was a phagostimulant for a snail, *Z. arboreus* (Hollingsworth & Armstrong 2003), we found no evidence that *L. floridana* would respond positively to neem oil; this may similarly reflect the more restricted dietary of this slug. Thus, the orthoboric acid formulation is not recommended for control of *L. floridana*, though it is effective for some other molluscs.

Overall, *L. floridana* is a resilient species, perhaps explaining why its geographic range continues to expand. It can survive and grow on several host plants, both cultivated and uncultivated, and also survive on less preferred plants and detritus. Though not as voracious as some other large molluscs (e.g., *Z. provisorio*) it nevertheless can cause considerable foliar injury and feed on numerous plant species. This species can be controlled successfully with some, but not all, conventional toxic bait treatments.

## Acknowledgments

The support of Universidade Estadual de Montes Claros – UNIMONTES, and Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq to CGR is gratefully acknowledged. We thank John Slipcinsky of the Florida Museum of Natural History for confirmation of slug identifications.

## References Cited

- Aguiar R, Wink M. 2005. How do slugs cope with toxic alkaloids? *Chemoecology* 15(3): 167-177.
- Baker HB. 1925. North American Veronicellidae. *Proceedings of the Academy of Natural Sciences, Philadelphia* 77: 157-184.
- Barker GM. 2001. Gastropods on land: phylogeny, diversity, and adaptive morphology, pp. 1-146 *In* Barker GM (ed.), *The Biology of Terrestrial Molluscs*. CABI Publishing, Wallingford, United Kingdom.
- Briner T, Frank T. 1998. The palatability of 78 wildflower strip plants to the slug *Arion lusitanicus*. *Annals of Applied Biology* 133(1): 123-133.
- Campbell BG, Little MD. 1988. The finding of *Angiostrongylus cantonesis* in rats in New Orleans. *American Journal of Tropical Medicine and Hygiene* 38(3): 568-573.
- Capinera JL. 2012. Culture of terrestrial slugs and snails (Gastropoda): acceptance and suitability of synthetic insect diets. *Florida Entomologist* 95(4): 1077-1085.
- Capinera JL. 2013. Cuban brown snail, *Zachrysia provisoria* (Gastropoda): damage potential and control. *Crop Protection* 52(1): 57-63.
- Chatfield JE. 1976. Studies on food and feeding in some European land molluscs. *Journal of Conchology* 29(1): 5-20.
- Diaz JH. 2010. Recently reemerging helminthic infections causing eosinophilic meningoencephalitis: neuroangiostrongyliasis, baylisascariasis, and gnathostomiasis. *Journal of Neuroparasitology* 1(1): 1-14.
- Davidson DH. 1976. Assimilation efficiencies of slugs on different food materials. *Oecologia* 26 (3): 267-273.
- Dundee DS. 1977. Observations on the veronicellid slugs of the southern United States. *Nautilus* 91(3): 108-114.
- Duval DM. 1971. A note on the acceptability of various weeds as food for *Agriolimax reticulatus* (Müller). *Journal of Conchology* 27(1): 249-251.
- Getz LL. 1959. Notes on the ecology of slugs: *Arion circumspectus*, *Deroceras reticulatum*, and *D. laevis*. *American Midland Naturalist* 61(2): 485-498.
- Gomes SR. 2007. Filogenia morfológica de Veronicellidae, filogenia molecular de *Phyllocaulis* Colosi e descrição de uma nova espécie para a família (Mollusca, Gastropoda: Pulmonata) (Ph.D Dissertação, Universidade Federal Do Rio Grande do Sul, Porto Alegre, Brazil).
- Gomes SR, Thomé JW. 2004. Diversity and distribution of the Veronicellidae (Gastropoda: Soleolifera) in the Oriental and Australian biogeographical regions. *Memoirs of the Queensland Museum* 49(2): 589-601.
- Heller J. 1990. Longevity in molluscs. *Malacologia* 31(2): 259-295.
- Holland KD, McDonnell MJ, Williams NSG. 2007. Abundance, species richness and feeding preferences of introduced molluscs in native grasslands of Victoria, Australia. *Austral Ecology* 32(6): 626-634.
- Hollingsworth RG, Armstrong JW. 2003. Effectiveness of products containing metaldehyde, copper or extracts of yucca or neem for control of *Zonitoides arboreus* (Say), a snail pest of orchid roots in Hawaii. *International Journal of Pest Management* 49(2): 115-122.
- Keller M, Killmann J, Edwards PJ. 1999. Palatability of weeds from different European origins to the slugs *Deroceras reticulatum* Müller and *Arion lusitanicus* Mabilie. 1999. *Acta Oecologica* 20(2): 109-118.
- Kozłowski J. 2005. Host plants and harmfulness of the *Arion lusitanicus* Mabilie, 1868 slug. *Journal of Plant Protection Research* 45(3): 221-233.
- Maceira D. 2003. Las especies de la familia Veronicellidae (Mollusca, Soleolifera) en Cuba. *Revista de Biología Tropical* 51(3): 453-461.
- Mølgaard P. 1986. Food plant preferences by slugs and snails: a simple method to evaluate the relative palatability of the food plants. *Biochemical Systematics and Ecology* 14(1): 113-121.
- Naranjo-García E, Willibaldo Thomé J, Castillejo J. 2007. A review of the Veronicellidae from Mexico (Gastropoda: Soleolifera). *Revista Mexicana de Biodiversidad* 78(1): 41-50.
- Nash MA, Thomson LJ, Hoffman AA. 2007. Slug control in Australian canola: monitoring, molluscicidal baits and economic thresholds. *Pest Management Science* 63(9): 851-859.
- Pérez-Harguindeguy N, Díaz S, Vendramini F, Cornellissen JHC, Gurvich DE, Cabida M. 2003. Leaf traits and herbivore selection in the field and in cafeteria experiments. *Austral Ecology* 28(6): 642-650.
- Pilsbry HA. 1948. Land Mollusca of North America (North of Mexico). *Academy of Natural Sciences of Philadelphia, Monograph* 3, part 2(2): 521-1113.
- Qvarnstrom Y, Sullivan JJ, Bishop HS, Hollingsworth R, Da Silva AJ. 2007. PCR-based detection of *Angiostrongylus cantonesis* in tissue and mucus secretions from molluscan hosts. *Applied and Environmental Microbiology* 73(5): 1415-1419.
- Raut SK, Ghose KC. 1983. The role of non-crop plants in the protection of crop plants against the pestiferous snail *Achatina fulica*. *Malacological Review* 16(1): 95-96.
- Rollo CD, Shibata DM. 1981. Resilience, robustness, and plasticity in a terrestrial slug, with particular reference to food quality. *Canadian Journal of Zoology* 69(4): 978-987.
- Rueda ARP. 1989. Biology, nutritional ecology, and natural enemies of the slug *Sarasinula plebeia* (Fischer 1868) (Soleolifera: Veronicellidae). Unpublished M.S. Thesis, University of Florida, 163 pp.
- Rueda A, Caballero R, Kaminsky R, Andrews KL. 2002. Vaginulidae in Central America, with emphasis on the bean slug *Sarasinula plebeia* (Fischer), pp. 115-144 *In* G. M Barker (ed.), *Molluscs as Crop Pests*. CABI Publishing, Wallingford, United Kingdom.
- Smith TR, White-Mclean J, Dickens K, Howe AC, Fox A. 2013. Efficacy of four molluscicides against the giant African snail, *Lissachatina fulica* (Gastropoda: Pulmonata: Achatinidae). *Florida Entomologist* 96(2): 396-402.
- South, A. 1992. *Terrestrial Slugs: Biology, Ecology and Control*. Chapman and Hall, London.
- Speiser B, Hochstrasser M. 1998. Slug damage in relation to watering regime. *Agriculture, Ecosystems and Environment* 70(2-3): 273-275.
- Speiser B, Kistler C. 2002. Field tests with a molluscicide containing iron phosphate. *Crop Protection* 21(5): 389-394.
- Teem JL, Qvarnstrom Y, Bishop HS, Da Silva AJ, Carter J, White-Mclean J, Smith T. 2013. The occurrence of the rat lungworm, *Angiostrongylus cantonesis*, in nonindigenous snails in the Gulf of Mexico region of the United States. *Hawai'i Journal of Medicine and Public Health* 72(6) supplement E: 11-14.
- Thomé, J. W. 1989. Annotated and illustrated preliminary list of Veronicellidae (Mollusca: Gastropoda) of the Antilles, and Central and North America. *Journal of Medical and Applied Malacology* 1(1): 11-28.
- Wang QP, Lai DH, Zhu XQ, Chen ZG, Lunn ZR. 2008. Human angiostrongyliasis. *Lancet Infectious Diseases* 8(10): 621-630.
- Willis JC, Bohan DA, Powers SJ, Choi YH, Park J, Gussin E. 2008. The importance of temperature and moisture to the egg-laying behavior of a pest slug, *Deroceras reticulatum*. *Annals of Applied Biology* 153(1): 105-115.
- Young AG, Port GR. 1991. The influence of soil moisture on the activity of *Deroceras reticulatum* (Müller). *Journal of Molluscan Studies* 57(1): 138-140.