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Biology and food habits of the invasive snail *Allopeas gracile* (Gastropoda: Subulinidae)

*John L. Capinera**

Abstract

The biology of the widely occurring but poorly known terrestrial snail *Allopeas gracile* (Hutton, 1834) (Gastropoda: Subulinidae) was determined, emphasizing food relationships. Isolated snails reproduced without cross fertilization. These snails deposited small clusters of eggs (3–7 per d) totaling about 20 per mo once oviposition commenced (after about 50 d). The snails grew rapidly for 50 d, attaining a mass of about 25 mg, then grew more slowly, eventually attaining a mass of about 50 mg after 250 d. Hatching occurred over a wide range of temperatures. The mean duration of the egg stage decreased from 18.7 to 8.0 d as the temperature increased from 19.5 to 32.0 °C. *Allopeas gracile* was omnivorous, feeding on green plants (vegetables, weeds, and flowers), fungi (cultivated mushroom and sooty mold), and animal matter (dead cockroaches and earthworms), but not decaying vegetation (tree leaves). Although this species is omnivorous, many plants allowed only maintenance, not fostering rapid growth. These small snails consumed only about 1.5 cm^2 per d of favored food (lettuce) at maturity, and considerably less of most plants offered. This invasive snail does not seem to be destined to be a significant pest except perhaps under restricted circumstances.

Key Words: feeding behavior; host; pest status; mollusk; mollusc; invasive pest

Resumen

Se determinó la biología del caracol terrestre, *Allopeas gracile* (Hutton), que es ampliamente distribuido pero poco conocido,enfatizando las relaciones alimentarias. Los caracoles aislados se reprodujeron sin fertilización cruzada. Estos caracoles depositaron pequeños grupos de huevos (3-7 por dia) por un total de aproximadamente 20 por mes una vez que comenzó la oviposición (después de aproximadamente 50 dias). Los caracoles crecieron rápidamente durante 50 dias, logrando una masa de aproximadamente 25 mg, luego crecieron más lentamente, alcanzando finalmente una masa de aproximadamente 50 mg después de 250 dias. La eclosión ocurrió en una amplia gama de temperaturas. La duración media del estadio del huevo disminuyó de 18,7 a 8,0 dias cuando la temperatura aumentó de 19,5 a 32,0° C. *Allopeas gracile* fue una omnívora, alimentándose de plantas verdes (hortalizas, hierbas y flores), hongos (hongos cultivados y fumigina) y materia animal (cucarachas muertas y lombrices de tierra), pero no de vegetación en descomposición (hojas de árbol). Aunque esta especie es omnívora, muchas plantas sólo permiten el mantenimiento y no se fomentó un crecimiento rápido. Estos pequeños caracoles consumían sólo alrededor de 1,5 cm2 por dia de alimentos favorecidos (lechuga) en la madurez, y considerablemente menos de la mayoría de las plantas ofrecidas. Este caracol invasor no parece estar destinado a ser una plaga significativa excepto quizás bajo circunstancias restringidas.

Palabras Clave: comportamiento alimentario; hospedero; estatus de plaga; molusco; molusco; plaga invasora

Allopeas gracile (Hutton, 1834) (Gastropoda: Subulinidae) occurs widely in tropical and subtropical areas of Asia, Australia, and Polynesia, as well as Central and South America. It has been introduced to many islands in the Caribbean region, and into much of the southeastern USA (Dundee 1971). It also sometimes occurs in temperate areas as a greenhouse inhabitant. Although described from India, Neck (1976) and Auffenberg & Stange (1988) suggested that its origin is South America. In much of the extant scientific literature it is known as *Opeas gracile* and *Lamellaxis gracilis*, and in the popular literature it is sometimes called graceful awl snail.

The economic status of *A. gracile* is uncertain. In Malaysia, it is reported to damage vegetables and tobacco (Jambari et al. 1999). In India, Raut & Ghose (1984) listed it as 1 of 7 mollusc pests and considered it to be probably the most widely distributed of the pest species. However, Mitra & Biswas (1974) and Mitra et al. (1976) considered it to be a minor pest of potted plants in India, feeding mostly on fallen and decomposing leaves, though fresh leaves of bael, *Aegle marmelos* (L.) Correa (Rutaceae) were consumed. In Louisiana, Dundee (1970) indicated that this species fed on hawksbeard, *Crepis* sp. (Asteraceae); Canadian woodnettle, *Laportea canadensis* (L.) Weddell (Urticaceae); and panicgrass, *Panicum* sp. (Poaceae). Mitra & Biswas (1974) reported that the feeding behavior on plant tissues varies considerably, depending on the plant species and age of the tissue. They also noted that *A. gracile* is necrophagous, but not predatory, feeding on dead snails and other animal protein.

Jambari et al. (1999) reported that *A. gracile* was more difficult to control than some other snail species because it entered the soil during the daylight hours. Management of terrestrial molluscs using toxic bait formulations is increasingly popular. However, not only must the toxicant be effective, but the bait must be suitably acceptable. Baits are not equally attractive. Capinera & Guedes Rodrigues (2015) reported that the leatherleaf slug *Leidyula floridana* (Leidy, 1851) (Gastropoda: Veronicellidae), although susceptible to the toxicant orthoboric acid when it was applied to foliage, was not affected when orthoboric acid

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was provided as a bait formulation (sold commercially as Niban®), seemingly because the slugs did not ingest the bait. On the other hand, the Cuban brown snail*, Zachrysia provisoria* (Pfeiffer, 1858) (Gastropoda: Pleurodontidae), consumed this same orthoboric acid–based bait and was readily killed (Capinera 2013).

Although it is found widely (some have claimed it to be the most widely distributed terrestrial snail, e.g., Pilsbry 1946), the habits of *A. gracile* are poorly documented. Only Dundee (1970, 1986) has devoted much attention to it in North America (in and near New Orleans, Louisiana), although Karlin (1956) assessed its damage potential to roses in greenhouses in the state of New York. Neck (1976) reported finding "high-density clusters in flower gardens" in Texas. This lack of attention probably is due to the lack of damage to crops, but also possibly because *A. gracile* is small and easily overlooked (Fig. 1), and hides in the soil during the daylight hours. Nonetheless, due to damage caused by invading organisms, including snails, inquiries about damage potential are commonly received in Florida. Thus, studies of the biology and damage potential of *A. gracile* were undertaken.

Materials and Methods

COLONY MAINTENANCE

The *A. gracile* colony was initially isolated from mulch in a flower garden in Gainesville, Florida. The stock colony was maintained in 25 × 18 × 10 cm (LWH) transparent plastic boxes with about 3 cm of garden soil, including leaf litter and bark chips, on the bottom. They were fed store-purchased romaine (cos) lettuce, *Lactuca sativa* L. (Asteraceae) ad libitum, and cultured at 25 °C and a 14:10 h L:D photoperiod. Garden lime suspended in gelled agar (20% lime by weight) was provided continuously as a dietary supplement to ensure shell growth.

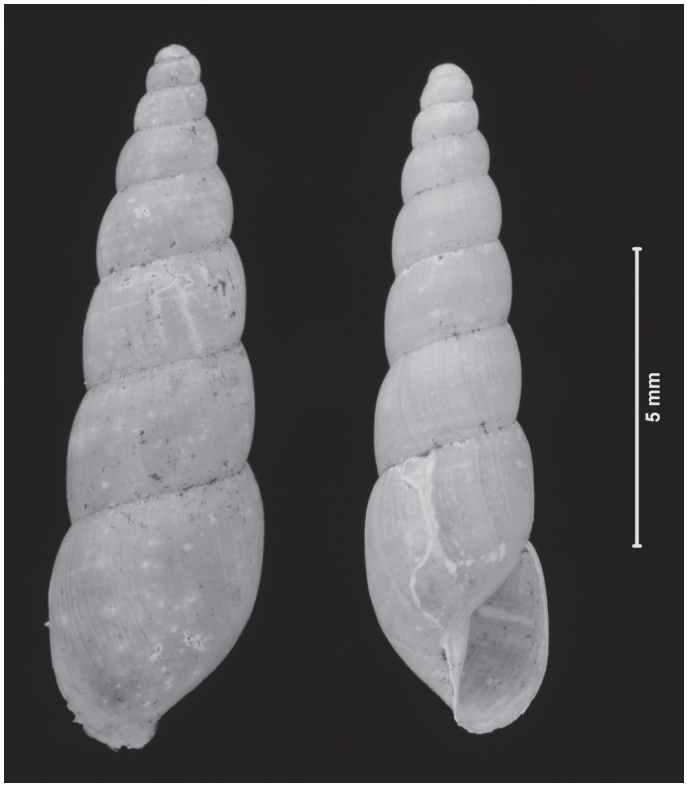


Fig. 1. Lateral view of *Allopeas gracile*, showing the characteristic elongate spire and aperature, and small size. Photo by L. Buss, University of Florida.

GROWTH AND DEVELOPMENT

The pattern of growth and development was determined by culturing individual snails from hatch until their growth stabilized at about 290 d. Environmental conditions were as described for colony culture. Each snail was cultured in a 30 mL plastic cup with a cardboard lid. Each cup also contained about 10 mL of moist soil and a small piece of lime-agar. The snails were fed with romaine lettuce once or twice per week depending on the rate of foliage consumption and the condition of the foliage. Mass and height of 20 snails were recorded at about 7 d intervals, with mass determined using a Mettler Toledo® A104 analytical balance (Mettler-Toldeo, LLC, Columbus, Ohio), and height using an ocular micrometer fitted to an Olympus® VMZ stereoscopic microscope (Olympus Corporation of the Americas, Center Valley, Pennsylvania). The soil was examined weekly for eggs and hatchlings. Monthly, the adult snails (judged by size, ≥7 mm height) were moved to clean containers and the old cups maintained for another 30 d to allow more snails to hatch so reproduction could be estimated per snail per month. Measurements of egg size were also made with the ocular micrometer.

Additional experiments were conducted to assess the effect of temperature on egg hatch because the hatching time reported by Jambari et al. (1999), which was stated to be 24 h, seemed inordinately short. Mature snails were held at 25 °C and a 14:10 h L:D photoperiod, and provided with fresh soil and lettuce, then moved daily to new soil in 30 mL containers. Eggs were maintained on moist soil at 1 of 6 constant temperatures: 19.5, 22.0, 24.5, 27.0, 29.5, or 32.0 °C. The eggs were maintained in complete darkness within Precision™ 816 incubators except for the brief daily checks for hatching. Newly hatched snails were removed, and the mean, standard deviation, median, minimum, and maximum number of days until hatch were determined for each temperature. Also calculated were the lower and upper 95% confidence intervals for the means.

HOST PLANT SELECTION

Acceptance of selected plants was evaluated by confining 1 mature snail (reproductive age) to a 30 mL cup with moist filter paper (2.5 cm in diameter) on the bottom, capped with a cardboard top that enclosed a disc (1 cm in diameter) of leaf tissue. In these no-choice tests, each diet item was tested with 4 replicates of 10 snails (40 snails) for 48 h at 25 °C and a 14:10 h L:D photoperiod. Replicates were conducted on different days using new snails and plant material. The numbers of snails in each replicate that nibbled on the leaf tissue (determined by microscopic examination), and the number that ate at least 10% (estimated by eye) of the disc were recorded. The numbers for both nibbling and higher levels of consumption were transformed by log (x + 1) and analyzed separately by 1-way ANOVA using the GraphPad Prism software (GraphPad Software, Inc., San Diego, California). The means were separated using the Bonferonni multiple comparison test.

The material tested for acceptance included leaf tissue from several vegetable crops: romaine (cos) lettuce, leaf (looseleaf) lettuce, *L. sativa*; iceberg (head) lettuce, *L. sativa*; spinach, *Spinacia oleracea* (Amaranthaceae); sweet potato, *Ipomoea batatas* (Convolvulaceae); nappa cabbage, *Brassica rapa pekinensis* (Brassicaceae); bok choy cabbage, *Brassica rapa chinensis* (Brassicaceae); collards, *Brassica oleracea* (Brassicaceae); kale, *B. oleracea*, and parsley, *Petroselinum crispum* (Apiaceae).

Also evaluated were several common weeds: creeping indigo, *Indigofera spicata* (Fabaceae); livid amaranth, *Amaranthus blitum* (Amaranthaceae); pokeweed, *Phytolacca americana* (Phytolaccaceae); American sicklepod, *Senna obtusifolia* (Fabaceae); wild poinsettia, *Poinsettia heterophylla* (Euphorbiaceae); white clover, *Trifolium repens* (Fabaceae); Old World diamond flower, *Hedyotis corymbosa* (Rubiace-

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ae); Brazilian pusley, *Richardia brasiliensis* (Rubiaceae); and common ragweed, *Ambrosia artemisiifolia* (Asteraceae).

Flowers evaluated were: French marigold, *Tagetes patula* (Asteraceae); windflower, *Gaillardia aristata* (Asteraceae), impatiens, *Impatiens walleriana* (Balsaminaceae); wax begonia, *Begonia semperflorens* (Begoniaceae); and scarlet salvia, *Salvia splendens* (Lamiaceae).

Because Mitra et al. (1976) indicated that *A. gracile* would eat green leaves, old green freshly fallen leaves, or decomposed leaves depending on the species of plant, a plant tissue age test was conducted to determine how plant leaf age affected acceptance. Leaf discs measuring 8 mm in diameter were punched from green (young) and yellow (senescent) vegetation collected from 4 species of plants: creeping indigo; perennial peanut, *Arachis glabrata* (Fabaceae); wild poinsettia; and common beggarticks, *Bidens alba* (Asteraceae). In these choice tests, a yellow and a green leaf disc were provided to 20 groups of 3 adult snails. The foliage was presented on moist filter paper in a Petri dish (9 cm in diameter, 1.5 cm high). The level of consumption of each disc was estimated visually (5% increments) after 48 and 96 h of exposure. The consumption data were arcsine transformed prior to analysis. Paired *t*-tests (GraphPad Prism software) were used to assess differences in consumption between the younger and older foliage.

The level of potential consumption was estimated using mature (reproductive) snails and romaine lettuce, a preferred host. Individual snails (n = 20) were isolated in 500 mL plastic cups with moist filter paper and a 5 × 5 cm section of lettuce leaf. After 24 h, the leaf area was determined with a LI-3000 leaf area meter (LI-COR® Biosciences, Lincoln, Nebraska). Then, the feeding sites were taped over with paper tape and the leaf was measured again. The difference in measurements was attributed to snail feeding.

HOST SUITABILITY

Suitability experiments were conducted by culturing 20 snails per diet, each in a separate 30 mL cup, as described previously for host selection experiments. These snails were newly hatched (generally 0.5–3.0 mg) and were maintained for 49 d. The suitability of each diet was assessed by plotting the weekly mean mass determinations and by comparing the initial mass with the 49 d mass using a paired *t*-test (GraphPad Prism software). Some snails died during the experiment; only data from individuals that survived 49 d were used in the calculations. Normality of the mass data was assessed with the D'Agostino and Pearson omnibus normality test (Graphpad Prism software). Nearly all data sets in the suitability experiments were Gaussian, so data were not transformed.

The plants tested for suitability included several vegetable crops: romaine lettuce leaves; leaf lettuce leaves, *L. sativa* (Asteraceae); bok choy cabbage leaves; nappa cabbage leaves; sweet potato leaves; Irish (white) potato leaves, *Solanum tuberosum* (Solanaceae); mustard leaves, *Brassica juncea* (Brassicaceae); sliced zucchini fruit, *Cucurbita pepo* (Cucurbitaceae); sliced Irish potato tuber; sliced carrot taproot, *Daucus carota sativus* (Apiaceae); and sliced white mushroom, *Agaricus bisporus* (Agaricaceae).

Also included in the suitability tests were several weeds and flowers. Weeds assessed were: livid amaranth; pokeweed; Brazilian pusley; wild radish, *Raphanus raphanistrum* L. (Brassicaceae); white clover; creeping indigo; a mixture of roots from 3 weeds: livid amaranth, Brazilian pusley, and bahia grass, *Paspalum notatum* (Poaceae); and a mixture of leaf tissue from 3 weeds: livid amaranth, creeping indigo, and pokeweed. Flowers evaluated were: French marigold, impatiens, windflower, wax begonia, and scarlet salvia.

Miscellaneous potential food sources, some of which served as controls for the potential natural diets, were: sooty mold (*Fumagospora* sp.; Capnodiaceae) growing on leaves of hackberry, *Celtis occidentalis* (Cannabaceae); freshly killed Surinam cockroaches, *Pycnoscelus surinamensis* (L.) (Blattodea: Blaberidae); pieces of freshly killed earthworm, *Eisenia* sp. (Annelida: Clitellata: Lumbricidae); biofilm (microorganisms adhering to bark chips removed from containers used to culture slugs); soil (garden soil rich in organic matter and including decaying tree leaves); and lime-agar (20% garden lime suspended in gelled agar).

ACCEPTANCE OF TOXIC BAIT FORMULATIONS

To determine the acceptance of baits, the efficacy of 4 toxic bait products was assessed under laboratory conditions. Groups of 10 mature snails were placed into 500 mL plastic cups containing moist paper towels and a 5 × 5 cm^2 section of romaine lettuce. Some containers also received 0.1 g of toxic bait: metaldehyde-based Corry's® Slug and Snail Pellets (Matson LLC, North Bend, Washington), orthoboric acid–based Niban® Granular Bait (Nisus Corporation, Rockford, Tennessee), iron phosphate–based Ecosense® Slug and Snail Killer (Ortho, Marysville, Ohio), or sodium ferric EDTA–based Ferroxx® Slug and Snail Bait (Neudorff North America, Brentwood Bay, Canada). A check (no bait) treatment was included as a control. The snails were allowed 48 h to consume the bait, then the bait was removed and the number of snails surviving was monitored at 2, 5, 10, and 15 d post treatment. Food was replaced at the aforementioned monitoring intervals and the damage (level of feeding) was assessed. Damage to lettuce was assessed using an index of 1 to 4, where 1 was no visible damage, 2 was less than 10 feeding sites, 3 was 10 to 20 feeding sites, and 4 was greater than 20 feeding sites. All treatments were replicated 5 times (50 snails per treatment), with different starting dates serving as the basis for replication. A repeated measures 2-way ANOVA (GraphPad Prism software) was used to assess the bait treatment and time factors. Significant differences in mean values were determined using the Bonferroni multiple comparison test.

Results

GROWTH AND DEVELOPMENT

Isolated *A. gracile* snails fed romaine lettuce grew rapidly during the first 50 d, attaining a mean height of over 8 mm and a mean weight of about 25 mg. Thereafter, the increase in height and weight continued, but at a much slower rate (Fig. 2). The snails eventually attained a fairly stable size (mean height of about 11 mm, mean weight of greater than 50 mg) after about 250 d. The largest snail encountered attained a height of 16.5 mm, but snails greater than 12 mm in height were rare. The weight of individual snails increased or decreased noticeably from week to week, depending on whether or not they had deposited eggs.

Maturation (initiation of egg production) coincided with the shift from rapid growth to slower growth. Some snails began producing eggs after about 50 d, although others required longer, about 60 d. Once initiated, egg production continued for the duration of the experiment, 280 d (9.3 mo), and probably would have continued longer. Eggs were deposited singly, but in loose clutches. Initially, egg clutches contained about 3 eggs, but they quickly began to average about 5 per clutch, eventually attaining about 7 per clutch. The eggs were white and spheroid, being slightly wider than high. The mean egg width (± SD) was 0.9 ± 0.1 mm, and the mean height was 0.8 ± 0.1 mm (n = 18), with a range of 0.6 × 0.5 mm to 1.2 × 1.1 mm (W × H). The mean egg weight (± SD) was 0.8 ± 0.1 mg (n = 22).

The mean number of progeny produced (± SD) per snail (n = 11 surviving 280 d) during the final 8 mo was 18.2 ± 7.5, 17.0 ± 6.7, 22.1 ± 10.3, 6.8 ± 3.9, 22.0 ± 8.7, 32.4 ± 12.8, 23.8 ± 8.6, and 11.2 ± 6.2

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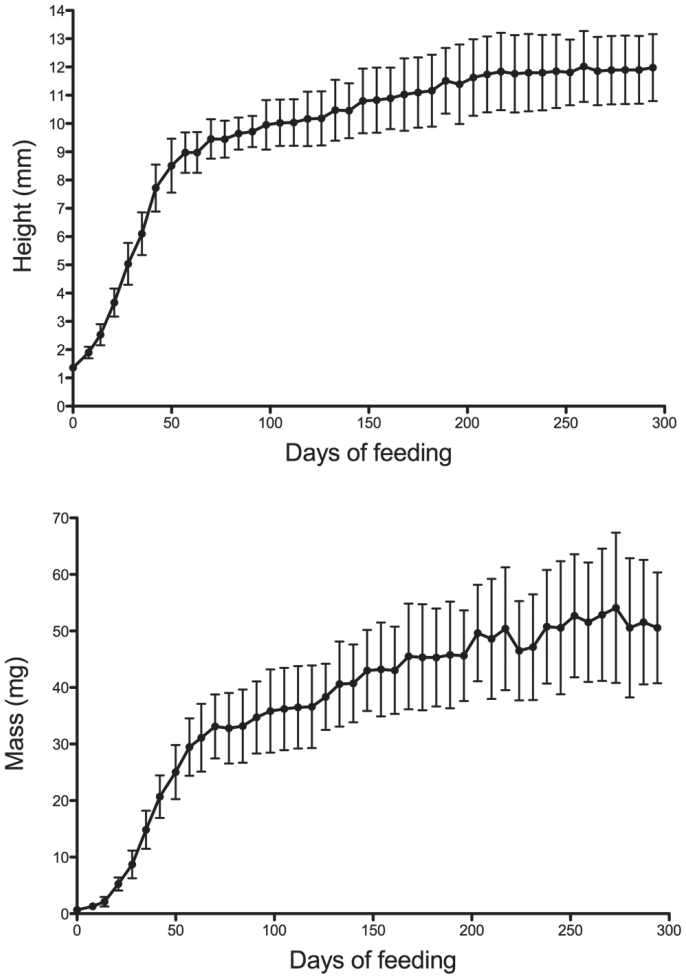


Fig. 2. Change in height (top) and mass (bottom) of *Allopeas gracile* over a 280 d period of culture.

per adult snail, respectively. Thus, the mean (± SD) number of progeny produced per snail was 153.4 ± 35.5, and the mean (± SD) number per month once reproduction commenced was 19.2 ± 14.4 progeny. All snails that reached adulthood (judged by size, ≥7 mm height) produced eggs, although some died before the experiment was terminated and these data were not included; however, during their life, the prematurely dying snails also produced similar numbers of eggs per month as the individuals that survived longer.

Egg clutches normally were deposited in soil at depths of about 1 cm. Under wet condition, however, individual eggs were found on the surface of the soil and on wood chips.

Temperature affected the length of time to egg hatch, but hatching occurred over a wide range of temperatures (Table 1). The mean duration of the egg stage decreased from 18.7 to 8.0 d as the temperature increased from 19.5 to 32.0 °C.

HOST PLANT SELECTION

When individual snails were offered a disc of vegetable, weed, or flower foliage in a no-choice test, they nibbled (detectable feeding but <10% consumption) on most of the plants (Table 2). Detectable feeding by at least 50% of the snails was observed on about 75% of the plant species tested. However, the ANOVA revealed that there were significant differences in consumption as determined by the number of snails nibbling on the plant foliage ($F = 22.26$; df = 23,72; $P < 0.001$). Protracted feeding (≥10% consumption) was much less frequent (Table 2); if we apply the same metric (feeding by 50% of the snails), only about 20% of plants were accepted. Similarly, the ANOVA revealed that there were significant differences in the number of snails displaying protracted feeding on different plants ($F = 21.10$; df = 23,72; $P < 0.001$). Most of the more acceptable plants, as judged by either nibbling or protracted feeding, were vegetable crops. However, some weeds were highly or moderately accepted, including livid amaranth, pokeweed, and wild poinsettia. Similarly, among flowers evaluated, French marigold and wax begonia were accepted to a limited degree.

Leaf age (green [young] versus yellow [senescent] foliage) in 4 plant species did not significantly affect consumption during the first 48 h (Table 3). However, when allowed additional time (an additional 48 h), during which the same plant tissues continued to degrade on the moist filter paper, the yellow (senescent) tissue became significantly more palatable than the green (younger) tissue.

The mature snails consumed a mean (± SD) of 1.46 (± 0.52) cm^2 per day when fed romaine lettuce. This is perhaps an imperfect estimate because in many instances they did not feed completely through the leaf, so it was difficult to measure reliably such consumption with the leaf area meter. This feeding behavior (called window pane feeding) typically involved snails feeding on the abaxial surface of the leaf, but leaving the adaxial surface intact. Thus, the upper leaf cuticle and epidermis remained intact (although nearly transparent), but the mesophyll and lower epidermis were consumed.

HOST SUITABILITY

Suitability of prospective vegetable hosts varied greatly. Among leaf tissues evaluated for snail growth, romaine lettuce was clearly superior to other plants (Table 4). Sliced zucchini, potato, carrot taproot, and white mushroom supported good growth, although the snails did not feed through the skin, feeding only where the tissue was sliced. However, in the case of ripe strawberry fruit, the snails were capable of causing fruit injury (unpublished observations; see Fig. 3), although other soft fruits were not tested. Less suitable vegetable plants in-

Table 1. Time (d) required for egg hatch by *Allopeas gracile* when maintained at 1 of 6 constant temperatures.

	Temperature (°C)					
Parameter	19.5	22.0	24.5	27.0	29.5	32.0
Minimum (d)	12	11	8	6	6	6
Maximum (d)	31	20	15	10	10	10
Mean (d)	18.7	15.7	11.4	8.8	8.6	8.0
SD of mean (d)	4.4	2.2	1.3	1.0	0.9	0.9
Median (d)	19	16	11	9	9	8
Lower 95% CI (d)	17.8	15.3	11.1	8.6	8.4	7.8
Upper 95% CI (d)	19.7	16.8	11.7	8.9	8.7	8.2
Number of eggs	87	109	85	148	87	121

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Table 2. Mean number (± SD) of *Allopeas gracile* snails displaying feeding, and number feeding on at least 10% of the foliage, when presented in the form of a 1 cm disc for a 48 h period.

Plant	Number feeding	Number feeding ≥10%
Leaf lettuce	8.75 ± 0.95a	8.25 ± 1.26a
Livid amaranth	8.50 ± 1.29ab	3.00 ± 0.82abc
Spinach	8.25 ± 0.50ab	1.25 ± 0.50cdef
Romaine lettuce	8.25 ± 1.71ab	7.50 ± 1.91ab
Pokeweed	8.00 ± 1.63ab	4.00 ± 0.81abc
Sweet potato	8.00 ± 1.83a	4.00 ± 1.41abc
Iceberg lettuce	8.00 ± 1.83ab	7.75 ± 1.50a
Nappa cabbage	7.75 ± 0.50ab	5.50 ± 0.58ab
Bok choy cabbage	7.50 ± 1.91ab	5.25 ± 0.96ab
Parsley	7.25 ± 0.96ab	1.50 ± 1.29cdef
French marigold	6.75 ± 0.50ab	3.00 ± 0.00abcd
Sicklepod	6.75 ± 0.95ab	2.00 ± 0.82bcde
Wax begonia	6.50 ± 1.29abc	2.25 ± 1.50bcde
Wild poinsettia	5.75 ± 1.71abc	2.50 ± 1.29bcde
Collards	5.50 ± 0.58abc	0.25 ± 0.50ef
Scarlet salvia	5.50 ± 0.58abc	1.00 ± 0.82cdef
Kale	5.25 ± 1.26bc	0.85 ± 0.95f
Creeping indigo	5.25 ± 0.95bc	3.75 ± 1.26abc
Impatiens	3.50 ± 1.00bc	0.00 ± 0.00
Windflower	3.25 ± 1.50cd	0.25 ± 0.50f
White clover	1.50 ± 1.29d	1.00 ± 1.41cdef
Old World diamond flower	0.50 ± 0.58d	0.00 ± 0.00f
Brazilian pusley	0.25 ± 0.50d	0.00 ± 00.0f
Common ragweed	0.00 ± 0.00d	0.00 ± 0.00f

Data were transformed by log (x + 1) for analysis but untransformed means are presented herein. Means followed by the same letter are not significantly different (P > 0.05).

cluded leaf tissue from sweet potato, Black-seeded Simpson lettuce, mustard, nappa cabbage, and bok choy cabbage (Fig. 4), but all allowed statistically significant growth by snails. Potato leaf tissue was not suitable for growth.

Leaf tissue from weeds also varied in suitability. A few, such as livid amaranth, Brazilian pusley, creeping indigo, and the weed leaf mixture supported statistically significant increases in snail weight, although others did not. The root mixture did not support vigorous growth of the snails. Overall, the weeds were not nearly as supportive of snail growth as were the vegetable crops (Table 4).

Flowers varied in their suitability for snail growth. French marigold, wax begonia, and scarlet salvia supported statistically significant growth, whereas impatiens and windflower did not (Table 4). Some other potential food sources also proved to be suitable, especially dead Surinam cockroaches, earthworms, and sooty mold (Fig. 5). Garden soil, biofilm, and lime-agar did not support growth (Table 4). The garden soil contained decaying leaf material (mostly elm, *Ulmus* sp. [Ulmaceae], and crape myrtle, *Lagerstroemia* sp. [Lythraceae]), so decayed leaf tissue is believed not to be a suitable food source.

ACCEPTANCE OF TOXIC BAIT FORMULATIONS

Survival differed significantly among the bait formulation treatments (F = 55.20; df = 4,20; P < 0.001). Time was also a significant factor in snail survival (F = 18.36; df =3,60; P < 0.001). The levels of survival are shown in Table 5, and it is evident that the Ecosense® and Ferroxx® baits were quite efficacious whereas survival in the Niban® treatment was not different from survival in the control (untreated) treatment. Survival in the Corry's® treatment was intermediate. In general, survival diminished over time. The interaction of treatment and time was not significant (F = 1.54; df = 12,60; P = 0.136).

Feeding on lettuce was significantly affected (Table 5) by the bait treatments (F = 52.38; df = 4,20; P < 0.001), although consumption in the Niban® treatment did not differ much from the control treatment. Feeding varied significantly with time (F = 5.65; df = 3,60; P < 0.002), mostly on the basis of increased feeding over time in the Niban® and Corry's® treatments. Thus, the interaction of bait treatment and time was significant (F = 3.55; df = 12,60; P < 0.001).

Discussion

Growth of *A. gracile* was studied previously by Subba Rao et al. (1981), but their experiments were conducted for only 6 wk, at which time reproduction commenced. They reported that newly hatched snails averaged 1.84 mm in height, with a range of 1.34 to 2.19 mm. I suspect that some were older, as the mean height of newly hatched snails in the present study was 1.31 ± 0.10 mm (± SD), with a range of 1.20 to 1.50 mm. After 6 wk, Subba Rao et al. (1981) reported a shell height of 4.25 mm. In contrast, in this study shell height at 6 wk was 7.72 ± 0.83 mm (± SD), suggesting that the unspecified diet provided by Subba Rao et al. (1981) was less suitable than the romaine lettuce diet.

Growth was also studied by Jambari et al. (1999), who determined snail height and weight for 27 wk. Their study used mustard as the food source, a plant that, although supporting growth in the present study, was not particularly favorable when evaluated relative to lettuce and several other potential foods. Thus, it is not surprising that Jambari et al. (1999) reported smaller heights (e.g., about 7 mm versus 10 mm) and lower mass measurements (e.g., about 22 mg versus 36 mg) at 15

Table 3. Mean percentage (± SD) of leaf disc consumption when *Allopeas gracile* snails were presented with a choice between relatively young (green) and senescent (yellow) foliage for 48 and 96 h.

		Consumption (%)			
Length of test (h)	Foliage color	Creeping indigo	Perennial peanut	Wild poinsettia	Common beggarticks
48	green	8.5 ± 6.8	1.4 ± 4.1	10.9 ± 18.7	2.3 ± 4.8
	yellow	4.6 ± 5.9	1.4 ± 3.0	9.2 ±15.5	1.5 ± 3.7
	t	1.144	0.017	0.419	0.722
	df	12	13	14	12
	P	0.275	0.987	0.681	0.484
96	green	14.6 ± 8.8	14.1 ± 20.2	12.1 ± 23.5	5.4 ± 7.2
	yellow	64.5 ± 25.1	63.6 ± 35.3	36.1 ± 34.3	82.7 ± 13.2
	t	4.587	4.207	2.775	11.890
	df	12	10	13	12
	P	<0.001	<0.002	0.016	<0.001

Statistics are t, df, and P values from paired t-tests at 48 and 96 h. Data were arcsine transformed for analysis, but untransformed data are presented herein.

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Table 4. Mean snail mass (mg ± SD) at beginning (day 0) and end (day 49) of study when fed a potential diet, and statistical significance (paired *t*-tests) of change in mass.

	Days of feeding		Statistics		
Diet	0	49	*t*	df	*P*
Zucchini slice	1.7 ± 0.7	26.9 ± 13.5	6.91	13	<0.001
Romaine lettuce	0.7 ± 1.6	25.0 ± 4.8	17.20	10	<0.001
Potato slice	1.0 ± 0.5	19.0 ± 9.3	6.06	10	<0.001
Cockroach	2.4 ± 1.4	17.1 ± 5.1	12.13	16	<0.001
White mushroom	1.6 ± 1.4	15.7 ± 9.8	5.75	14	<0.001
Carrot slice	1.2 ± 0.1	11.5 ± 4.5	9.85	16	<0.001
Sooty mold	1.6 ± 1.2	10.5 ± 3.6	7.27	10	<0.001
Sweet potato leaf	1.5 ± 0.6	10.5 ± 3.9	8.16	12	<0.001
Earthworm	1.5 ± 0.4	9.8 ± 6.3	4.24	10	0.002
Mustard	2.1 ± 1.2	8.1 ± 6.5	2.88	9	0.002
Leaf lettuce	2.9 ± 1.0	7.4 ± 4.6	3.98	12	0.002
French marigold	2.2 ± 0.7	7.3 ± 5.1	3.45	12	0.005
Bok choy cabbage	2.6 ± 1.3	6.9 ± 2.5	7.34	10	<0.001
Creeping indigo	2.7 ± 0.7	5.8 ± 4.1	2.99	13	0.011
Weed leaf mix	0.8 ± 0.3	5.5 ± 4.5	3.92	14	0.002
Nappa cabbage	2.2 ± 0.8	5.3 ± 2.5	4.89	11	<0.001
Wax begonia	2.3 ± 0.9	4.3 ± 2.2	3.87	15	0.001
Brazilian pusley	2.6 ± 0.7	3.9 ± 1.7	3.37	14	0.004
Scarlet salvia	2.3 ± 0.7	3.7 ± 1.0	5.43	15	<0.001
White clover	2.9 ± 0.5	3.4 ± 0.5	0.99	11	0.341
Livid amaranth	2.9 ± 1.5	3.3 ± 1.5	3.16	14	0.008
Root mix	2.6 ± 1.1	3.2 ± 1.2	2.00	14	0.065
Pokeweed	2.7 ± 1.1	2.9 ± 1.1	0.82	12	0.424
Lime-agar	2.7 ± 1.0	2.7 ± 1.1	1.23	15	0.238
Impatiens	2.3 ± 0.9	2.6 ± 1.1	1.22	12	0.247
Windflower	2.4 ± 1.0	2.4 ± 1.1	0.35	12	0.733
Wild radish	1.8 ± 0.8	2.3 ± 0.7	2.02	12	0.662
Biofilm	2.3 ± 1.4	2.3 ±1.6	0.13	12	0.898
Potato leaf	1.7 ± 1.2	1.8 ± 1.2	0.27	11	0.793
Soil	1.8 ± 0.5	1.7 ± 0.9	0.28	10	0.781

wk. However, the most curious feature of the study by Jambari et al. (1999) was that they reported that snails hatched from eggs within 24 h. This seemed highly improbable, so hatching times were determined at several temperatures. The results showed that hatching required several days at 6 examined temperatures, with development time inversely related to temperature (Table 1). Consistent with these observations, Biswas et al. (1976) reported hatching after 10 d, although the temperature to which the eggs were exposed was unspecified. Similarly, Dundee (1970) suggested an incubation period of 7 to 10 d.

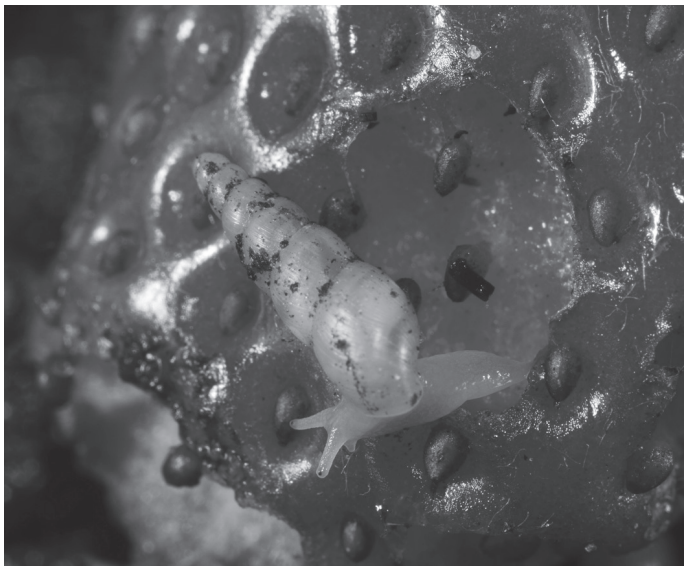


Fig. 3. *Allopeas gracile* feeding on ripe strawberry fruit. Photo by L. Buss, University of Florida.

Fecundity was previously studied by Subba Rao et al. (1980), who reported a mean total fecundity of 131 eggs per snail. However, the snails survived an average of only 123 d, so it is not surprising that the fecundity reported herein (153 eggs per snail) was higher, as these snails remained alive and were producing eggs even at 280 d. Note, too, that the means of estimating fecundity varied between the 2 studies. Subba Rao et al. (1980) counted eggs, whereas I counted young snails. The snails are easier to find in soil than the eggs, but some eggs may not have been viable. Dundee (1970), working in Louisiana, reported a mean of only 79 eggs per snail per breeding season, with most snails living for about 1 yr. Although the reproductive rates vary among studies, all indicate that snails reproduce even when isolated for their entire life, so cross fertilization is not required. Interestingly, Subba Rao et al. (1980) reported that up to 17 eggs could be deposited by a snail in a 24 h period, and Biswas et al. (1976) indicated that up to 14 eggs could be found in a clutch. In my observations, the number of eggs visible within the shell never exceeded 7, and egg deposition in 24 h never exceeded 7. However, when more than 1 snail was present, larger egg clutches could be found, presumably due to more than 1 snail selecting the same oviposition site. Oviposition occurs mostly in

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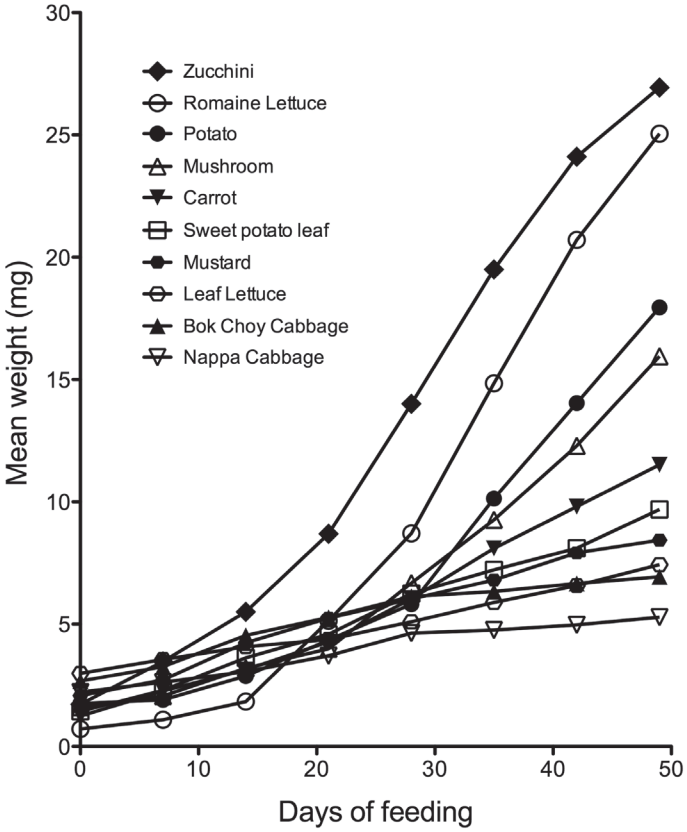


Fig. 4. Growth curves of *Allopeas gracile* when cultured for 49 d on selected vegetable fruits or foliage.

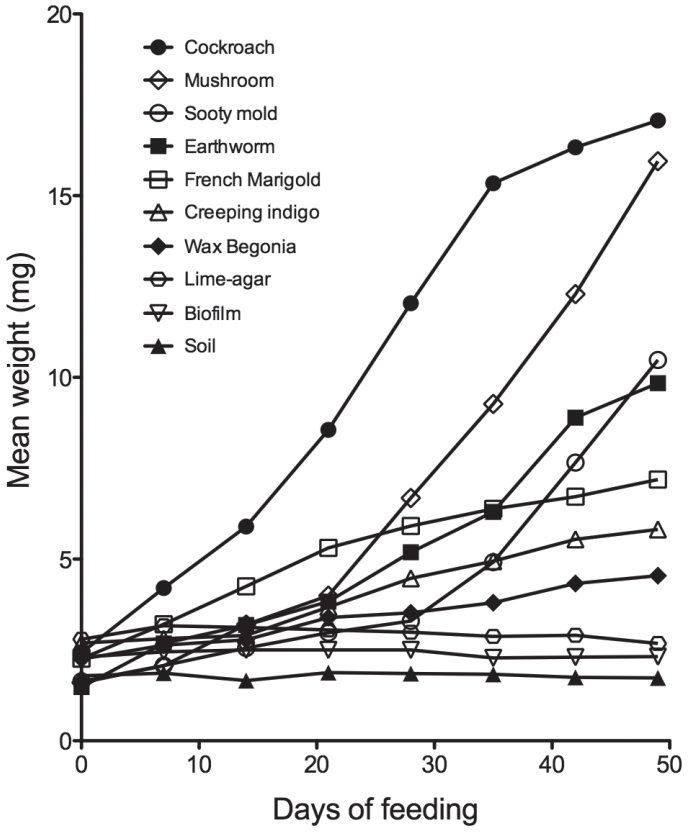


Fig. 5. Growth curves of *Allopeas gracile* when cultured for 49 d on selected weed or flower foliage, animal tissue, or other potential food. Soil and lime-agar served as controls, as these were available to all snails.

the warmer, wetter months of spring and summer (Dundee 1970; Raut 1984); apparently, snail activity diminishes in the winter months. This pattern of reduced oviposition during the winter occurs even under laboratory conditions.

The diet experiments demonstrated that although *A. gracile* will nibble (sample) most of the leaf tissue they encounter, their propensity to feed to a measurable degree (at least 10%) is much less. In short-term no-choice tests, the mean number of snails per replicate displaying detectable feeding was 5.7 (57%). In contrast, when the selection criterion was ≥10% leaf consumption, only 27% attained this threshold of consumption (Table 2). In many cases, the nibbling occurred only at the edges of the disc, and would not have been visible without microscopic examination. This is not typical feeding behavior; with acceptable hosts, the snails rasp away the leaf surface, with the feeding damage resembling that caused by adult flea beetles or neonate lepidopteran larvae, eventually leaving skeletonized or window pane leaf tissue—not much more than veins with thin strands of leaf tissue, or a thin layer of leaf epidermis, connecting the veins.

The diet experiments also demonstrated that the age of foliage influenced feeding by *A. gracile*. When offered detached foliage from 4 plant species, the snails initially (within 48 h) did not consume much of either the young (green) or the senescent (yellow) foliage (Table 3). Allowed additional time (an additional 48 h) for the foliage to degrade, however, the snails consistently chose the older yellow tissue over the younger green tissue in choice tests. These observations are consistent with the report by Mitra et al. (1976), who observed that although

Table 5. Mean (± SD) survival (number alive per 10 snails) and mean (± SD) level of 24 h feeding on lettuce (scale of 1 to 4 where 1 is no feeding) by *Allopeas gracile* at 2 to 15 d post treatment when fed toxic baits.

		Toxic bait treatments				
Variable	Day	Control	Niban®	Corry's®	Ecosense®	Ferroxx®
Survival	2	10.0 ± 0.0a	10.0 ± 0.0a	4.2 ± 2.3b	2.0 ± 1.2c	1.6 ± 1.1c
	5	10.0 ± 0.0a	8.6 ± 1.9a	4.2 ± 2.3b	1.0 ± 1.0c	0.6 ± 0.5c
	10	9.4 ± 0.9a	8.4 ± 2.2a	4.0 ± 2.4b	0.0 ± 0.0c	0.0 ± 0.0c
	15	8.8 ± 0.8a	7.6 ± 2.2a	4.0 ± 2.4b	0.0 ± 0.0c	0.0 ± 0.0c
Feeding	2	3.6 ± 0.5a	2.0 ± 0.7b	1.0 ± 0.0b	1.2 ± 0.4b	1.0 ± 0.0b
	5	3.8 ± 0.4a	3.2 ± 1.1a	1.8 ± 0.4b	1.0 ± 0.0b	1.0 ± 0.0b
	10	3.8 ± 0.4a	3.6 ± 0.5a	2.0 ± 1.0b	1.0 ± 0.0b	1.0 ± 0.0b
	15	3.4 ± 0.5a	3.0 ± 0.7a	2.6 ± 1.1a	1.0 ± 0.0b	1.0 ± 0.0b

Means within a row followed by the same letter are not significantly different ($P > 0.05$).

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fresh leaves of some plants were consumed, snails more often preferred "fallen" or "decomposed" leaves. Preferential consumption of senescent leaf tissue is not unusual in terrestrial molluscs, although Capinera (2013) reported that in the snail *Z. provisoria*, the young, green tissue was consumed preferentially for favored host plants, whereas senescent tissue was more readily consumed when the host plants were less favored.

Clearly, *A. gracile* can gain mass when fed several types of foliage from cultivated plants, and even some weeds. The mass gains associated with the vegetable fruits, namely sliced zucchini, potato, and carrot, were surprisingly high. However, I was not able to detect signs of feeding by snails through the epidermis of these fruits, even in no-choice tests. It appears that it would take a wound, perhaps from an insect or other gastropod, to allow feeding on these fruits by *A. gracile*. Dead cockroaches and earthworms supported good mass gain. Fungi also proved to be suitable food; both white mushroom and sooty mold supported appreciable weight gain. Among the top 10 food sources for mass gain, 3 were green leaf tissue, 3 were vegetable fruit slices, 2 were fungi, and 2 were animal tissue. At least in the laboratory, *A. gracile* had omnivorous dietary habits, which is consistent with previous reports. Omnivory can be a substantial advantage for invasive species; even if the rate of mass increase is modest, the numerous potential food sources should allow young snails to survive for long periods of time, perhaps until a more favorable food resource germinates or otherwise becomes available.

Although the snails consumed some of the toxic bait formulations, as judged by snail mortality and lettuce leaf consumption, the products evaluated were either not equally acceptable or not equally toxic. The Ecosense®, Ferroxx®, and Corry's® baits provided similar levels of leaf protection, although the metaldehyde-based Corry's® bait did not induce as high a level of mortality. Jambari et al. (1999) also reported difficulty in obtaining control of *A. gracile* with metaldehyde. However, here I report that *A. gracile* was somewhat susceptible to the Corry's® bait, and the snails were visibly attracted to the bait. In strong contrast, the Niban® bait was not very effective, generally not differing from the untreated control. I observed a slight trend of decreasing survival with time, but not much of a decreased consumption of lettuce. Thus, it does not appear that the Niban® treatment was readily consumed.

In a previous study, Capinera & Guedes Rodrigues (2015) reported that the leatherleaf slug *L. floridana* was not much affected by the Niban® bait, and attributed this result to the failure to accept the bait, because when the toxicant (orthoboric acid) was applied to foliage, the slugs readily consumed the toxicant and perished. A similar problem occurred here, as the 3 efficacious formulations all absorbed moisture rapidly and were visibly attractive to *A. gracile* snails soon after introduction into their containers, whereas the Niban® bait did not seem to attract the snails in the same manner. Also, when 5% orthoboric acid was sprayed onto lettuce and fed to *A. gracile* snails, higher levels of mortality ensued (unpublished observation).

Overall, *A. gracile* snails are clearly omnivorous. The feeding habit of *A. gracile* meets the criteria for polyphagy (multiple plants from multiple families; Bernays & Chapman 1994), but because weight gain was often minimal in the growth experiments, the degree of polyphagy is somewhat uncertain. These snails do not seem likely to cause much plant damage unless they become unusually numerous and come into association with highly attractive and suitable plants such as lettuce. Indeed, conspicuous feeding on crop plants was evident only with the vegetables, fungi, and French marigold. The small size, low level of foliar consumption, and dietary preferences work against this species becoming a significant pest. This species does not need to mate to reproduce regularly, which likely accounts for its worldwide distribution, as relocation of even a single snail could result in establishment of a new population. Should this species become damaging, some conventional toxic bait formulations can provide suppression, although it is advisable to select those that are most palatable.

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