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# SOME LIFE HISTORY TRAITS AND DIET SELECTION IN *PHILOMYCUS CAROLINIANUS* (MOLLUSCA: GASTROPODA: PHILOMYCIDAE)

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ABSTRACT

*Phylomycus carolinianus* (Bosc, 1902), (Mollusca: Gastropoda: Philomycidae) also known as Carolina mantleslug, is a widespread but poorly known terrestrial mollusc. We conducted studies to assess key aspects of its natural history. In the laboratory, its pattern of growth followed a sigmoid curve, but the growth rate was highly variable. Using a hierarchical clustering analysis of time to achieve reproductive maturity, the individual slugs could be separated into 4 discrete developmental groups: fast, intermediate, and slow-growing individuals, and also some that failed to develop completely. The 3 groups of developing slugs achieved reproductive maturity in about 129, 173, and 217 days, respectively. This developmental polymorphism suggests intra-generation risk-spreading. Reared alone or in pairs, slugs produced eggs in about 6 months; eggs numbered about 65 per cluster, though paired slugs produced slightly more eggs per cluster. Thus, these hermaphroditic slugs are capable of self-fertilization. Eggs hatched in about 3 weeks. Embryonic development occurred across the entire temperature range (10-29 °C) tested. The proportion of embryos developing was higher at 10, 14, 17 and 21 °C than at 25 and 29 °C. However, the embryos that developed at 10 and 29 °C did not hatch. Eggs incubated at 14 °C had the longest pre-hatching period, with those held at 25 °C the shortest. Synthetic gypsy moth and spruce budworm diets, and white mushrooms, all favored weight retention by adult slugs more than some natural diets tested, though mature slugs fed several diets produced eggs. Culture conditions of 21 °C and either gypsy moth or spruce budworm diet seemed optimal for growth and survival. Nearly all of the 51 mushroom species (representing 18 families) presented to slugs were eaten, though some much more readily than others. Except for Romaine lettuce, none of the foliage from 37 green plants offered were accepted as food.

Key Words: Carolina mantleslug, terrestrial molluscs, growth, development, diets, bet-hedging, hermaphroditism

RESUMEN

*Phylomycus carolinianus* (Bosc, 1902), (Mollusca: Gastropoda: Philomycidae) también conocido como la babosa del manto de Carolina, es un molusco terrestre ampliamente distribuido pero poco conocido. En el laboratorio, su patrón de crecimiento siguió una curva sigmoidea, pero la tasa de crecimiento fue muy variable. Utilizando un análisis de agrupación jerárquica del tiempo para alcanzar la madurez reproductiva, los individuos de babosas podrían ser separados en 4 grupos distintos de desarrollo: Individuos que crecen rápido, intermedio y lento, y los que no se desarrollan. Los 3 grupos de babosas en desarrollo alcanzaron la madurez reproductiva en aproximadamente 129, 173 y 217 días, respectivamente. Este polimorfismo en el desarrollo sugiere un reparto de riesgo intra-generacional. Criados solitarios o en parejas, las babosas producieron los huevos en unos 6 meses, con unos 65 huevos por grupo de huevos, aunque las babosas pareadas producen ligeramente más huevos por grupo. Por lo tanto, estas babosas hemafroditas son capaces de auto- fertilización. Los huevos eclosionaron en aproximadamente 3 semanas. El desarrollo embrionario sucedio a través de todo el rango de las temperaturas (10-29° C) probadas. La proporción de embriones en desarrollo fue mayor a los 10, 14, 17 y 21 ° C que a los 25 y 29 °C. Sin embargo, los embriones que se desarrollaron a los 10 y 29 °C no eclosionaron. Los huevos incubados a los 14 °C presentaron el período de pre-incubación más largo, con los mantenidos a los 25 °C el periodo más corto. Las dietas sintéticas de la polilla gitana y el gusano de brote de picea, y champiñones blancos, favorecieron la retención del peso de las babosas adultas más que algunas dietas naturales probadas, aunque babosas maduras alimentadas con varias dietas produjeron huevos. Casi todas las especies de champiñones que se presentaron a las babosas fueron consumidos, aunque algunos mucho más fácilmente que otros. Con la excepción de la lechuga romana, las plantas verdes no fueron aceptadas como alimento.

Palabras Clave: babosa de manto de Carolina, crecimiento, desarrollo, dietas, reparto de riesgo, hemafroditismo

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Slugs of the family Philomycidae possess a large empty shell sac, and a mantle that extends over the entire dorsal surface (Burch 1962). The type genus (*Philomycus* Rafinesque, 1820) is well represented in North America by *Philomycus carolinianus* (Bosc, 1902), also known as the Carolina mantleslug. It is a widely distributed member of this genus and is found across eastern North America from Canada to Florida and west to Iowa and eastern Texas (Pilsbry 1948). These large slugs (75-100 mm in length at maturity) typically dwell beneath the loosened bark of trees and decaying logs in humid, undisturbed forests (Pilsbry 1948; South 1992). Decayed beech, birch, basswood and other hardwood trees are typically preferred (Ingram 1949). *P. carolinianus* has been documented to consume several genera of mushrooms (Ingram 1949), and in the laboratory, lettuce (Pilsbry 1948).

Though normally found in forests, on occasion these slugs may be observed foraging in the open, and *P. carolinianus* and other species in the genus *Philomycus* have been observed crawling down trees from as high as 8 m (Keller & Snell 2002). Like most slugs, normally they are active at night, but also may be active under cloudy and humid conditions. Ingram (1949) considered *P. carolinianus* to be an aggregating species, but Pearce & Porter (2011) showed that aggregation was an incidental result of shelter-seeking behavior, and there was not a statistically significant degree of aggregation. Unlike some slugs, members of this species are not aggressive toward one another. They produce copious amounts of slime even when not disturbed.

Slugs are important in decomposition of organic materials, and are a food resource for many vertebrates. The biology and life history traits of *P. carolinianus* are poorly known. The goal of this study was to enhance our knowledge of its biology by documenting some developmental and reproductive characteristics of *P. carolinianus* under laboratory conditions, as well as by examining its dietary habits.

## Materials and Methods

### Growth

For growth studies, 6 clutches of eggs were obtained from *P. carolinianus* that were field-collected from separate mesic, upland mixed forests in Gainesville, Florida (Florida Natural Areas Inventory 1990). In this experiment, each replicate consisted of one of these egg clutches, which averaged about 60 eggs per clutch (a total of 356 eggs hatched successfully). The clutches were incubated between moistened paper towels in a cylindrical plastic container (18.5 cm diam. × 7.5 cm high). Upon hatching, juveniles were promptly removed from the incubation chamber and placed individually into vented cylindrical plastic containers (9.5 cm diam. × 4.5 cm high). The slugs were fed gypsy moth diet (Bio-Serv, Frenchtown, New Jersey) from hatching to reproductive maturity (time of first oviposition). A moistened paper towel was placed in each container to maintain humidity, and each juvenile was weighed at the time of hatch and at 3-day intervals. The slugs were provided with fresh food and transferred to a clean container once per week, maintained at 21 °C ± 1 °C with a photoperiod of 12:12 h L:D, and observed for 9 months.

There was considerable variation in weight gain and the length of time to reproductive maturity among individuals within each replicate, and it appeared that the slugs remaining alive for the duration of the experiment could be visually separated into distinct developmental groups. Therefore, a hierarchical clustering analysis of time to achieve reproductive maturity (average weight at initiation of oviposition) based on Ward's minimum variance method was used to sort the population data into groups with similar developmental rates, and analyzed using Statistical Analysis System (SAS®), JMP – Version 8 software (SAS Institute, Inc. 2008). The separation was conducted based on the degree of similarity (i.e., the shortest distance between values).

A one-way analysis of variance (ANOVA) was used to determine if there were any significant differences among the times to reproductive maturity (initial production of eggs) for groups discerned by the clustering analysis. Time to reproductive maturity was compared among groups using Tukey's post hoc multiple comparison test. Data met normality assumptions and were not transformed.

### Fecundity

Oviposition date and clutch size of 124 clutches (7266 eggs in total) collected from self-fertilizing specimens in the growth experiment were recorded. Each clutch was incubated in a separate cylindrical container (18.5 cm diam × 7.5 cm high), between a folded, moistened paper towel. The eggs were held for 30 days in an incubator at 21 °C in the dark. Eggs were considered to be not viable if no embryonic development was observed at the end of this period, but were included in pertinent calculations (number of eggs, mean proportion that hatched). Hatching date and the number of hatchlings per clutch were recorded.

A second experiment was conducted to evaluate changes in mean clutch size and mean hatching success in successive clutches. Thirty adults from the aforementioned growth experiment were randomly selected, and clutch size and hatching success determined for the first 6 successive clutches produced by each self-fertilizing animal. Spearman correlation analysis was conducted to deter-

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mine if there was a relationship between clutch size and sequence, and between the proportion of eggs that hatched and clutch sequence.

### Influence of Pairing

The objective of this experiment was to evaluate reproductive parameters of *P. carolinianus* when reared as solitary or paired specimens under laboratory conditions. Clutches laid by 3 field-collected slugs were used to initiate the experiment. Upon hatching, 72 juveniles (F1 progeny) were randomly selected from the 3 clutches to make 36 pairs. Each pair was placed into vented plastic containers (9.5 cm diam × 4.5 cm high) lined with moistened paper towel and kept separate from other specimens for the duration of the experiment. The slugs were fed gypsy moth diet (Bio-Serv, Frenchtown, New Jersey) *ad libitum*, and held at 21 °C with 12:12 h L:D. The eggs from all clutches produced by the paired slugs over a 9-month period were collected and incubated separately. The following parameters were recorded: number of eggs per clutch, mean percent hatching, and mean incubation period (days between egg deposition and hatching). In addition, the pre-oviposition period and the time between oviposition events of each pair of slugs were documented.

These reproductive parameters were also obtained for 82 randomly selected slugs selected from the same source but reared in isolation under otherwise identical conditions. These parameter values were then compared with those of the paired specimens. Two-sample t-tests were used to compare reproductive parameters between solitary and paired specimens, using SAS®.

### Temperature and Egg Development

The objective of this experiment was to estimate upper and lower temperature thresholds for *P. carolinianus* embryonic development. The eggs used in this experiment were collected from a laboratory colony of *P. carolinianus* maintained at 21 °C, with a photoperiod of 12:12 h L:D and fed gypsy moth diet *ad libitum*. Six constant temperatures (10, 14, 17, 21, 25 and 29 °C) were evaluated using 30 egg clutches per temperature (1 clutch = 1 replicate). The clutches were immediately removed from the adult rearing containers after deposition and each was incubated in a cylindrical plastic container (15 cm diam × 6.5 cm high) between sections of a folded, moistened paper towel and misted with tap water every 5-7 days to ensure that the eggs did not desiccate.

Six insect rearing chambers (Percival, Boone, Iowa) were used for incubation, each set at one of the experimental temperatures. Mean percent hatching and the mean time to hatching were documented. The mean percentages of embryos that developed (as determined by visual inspection) but did not hatch during the course of the experiment were also recorded. The eggs were classified as alive if they met all of the following criteria: the unhatched embryo responded to tactile stimuli; the embryo was strongly pigmented; and the tentacles were obvious and dark-colored. If at least one of these parameters was not met, the egg was considered dead, and was excluded from the pertinent calculations. The eggs evaluated in this experiment were incubated until eclosion or for a maximum of 180 days. A one-way analysis of variance (ANOVA) was used to test for differences in the mean percent egg development per clutch, mean percent egg hatch per clutch, and mean time to eclosion per clutch among temperature treatments. Significant differences among mean values were determined using Tukey's post hoc multiple comparison. Data met normality assumptions and were not transformed.

### Suitability of Diets

The objective of this experiment was to determine the appropriateness of several natural or artificial foods for short-term maintenance of laboratory colonies of *P. carolinianus*. Based on successful rearing of terrestrial molluscs by other investigators (Brooks et al. 2003; Faberi et al. 2006; Keller & Snell 2002; Capinera 2012), several potential diets were selected for evaluation. Diets selected were 4 natural diets: (1) romaine lettuce (*Lactuca sativa* var. *longifolia*, (2) carrot, (3) rabbit pellets, (4) white mushroom (*Agaricus bisporus*), plus 2 synthetic diets: (5) gypsy moth diet, and (6) spruce budworm diet. A seventh treatment group of unfed slugs were maintained under the same conditions except that no food source was provided. This was included to evaluate the effect of a lack of a food source on slug weight.

The slugs used in this experiment were selected from a laboratory colony reared on gypsy moth diet. There were 30 adult slugs per diet treatment. All were starved for 5 days prior to the experiment to void the gut. Slugs were determined to be adults based on the production of at least one clutch of eggs prior to this experiment, while fed gypsy moth diet. Each slug was weighed (precision = 0.1 mg) and placed individually in a clear, vented plastic container (9.5 cm diam × 7.5 cm high) with moistened paper towel for increased humidity.

The containers were arranged in a completely randomized design (7 rows and 30 columns) on a laboratory bench with an ambient temperature of 22 °C. Slugs were weighed once every 7 days for 8 weeks, at which time each was returned to a clean container with fresh gypsy moth diet as food source. Number of egg clutches and mortality were recorded daily. A one-way analysis of variance (ANOVA) was used to test for significant differences among treatments for the following

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parameters: final weight of the slugs, number of clutches, and percent mortality while fed the alternate diets. Significant differences between mean values were detected using a Tukey's post hoc multiple comparison test. Data met the normality assumptions and were not transformed.

### Preference for Mushrooms

The goal of this experiment was to determine the taxa of mushrooms that would most likely be consumed by *P. carolinianus* in natural habitats. A total of 51 mushroom species in 18 families, and a single species of lichen, were collected from areas where natural populations of *P. carolinianus* exist. These were evaluated as possible host material under laboratory conditions. An acceptability index was established for each potential food source by comparing consumption of each test mushrooms to a control (white mushroom). This technique is commonly used for assessing diets of slugs (e.g., Dirzo 1980; Rathcke 1985; Brooks et al. 2003).

Adults of *P. carolinianus* were maintained at 22 °C. Prior to the initiation of this experiment, the slugs were fed gypsy moth diet, and had not been exposed to any natural foods. They were not starved because we did not want them to be so hungry that they ate the first host they encountered; rather, we wanted them to sample the food resources available and choose the preferred host. Slugs were placed individually in a cylindrical, plastic container (9 cm diam × 4.5 cm high) with a single moistened paper towel to maintain humidity. Fresh mushrooms were provided for each test, with the commercially available white mushroom *(Agaricus bisporus* (J.E.Lange) Emil J. Imbach; Agaricales: Agaricaceae) as the control. Mushrooms were cut into similar dimensions, weighed, and then arranged so one piece each of a test and control mushroom were located in close proximity and equidistant from the slug. Ten replicates (one slug/container) were used per mushroom or lichen treatment. No slug was used to evaluate more than one species of test mushroom.

Five control containers were set up similarly with a pair of mushroom pieces, but without a mollusc, to calculate weight loss or gain of each mushroom. Tests were initiated in the afternoon, as slugs are more likely to feed during the evening. They were examined the following morning (after approximately 18 h), and every h after until at least 50% of either the test or control had been consumed. The mushroom pieces (control and test) were then weighed (precision = 0.1 mg).

The following acceptability index was used to evaluate feeding preference:

Acceptability Index:

$$\text{A.I.} = \frac{\text{Quantity of test mushroom eaten (g)}}{\text{Quantity of both mushrooms eaten (g)}}$$

Where,

A.I. = 0, test mushroom is unacceptable

A.I. = 0.01-0.44, test mushroom is slightly acceptable

A.I. = 0.45-0.55, test mushroom is moderately acceptable

A.I. = 0.56-1.0, test mushroom is highly acceptable

The change in mean weight of each species of mushroom tested in the control containers was used to adjust consumption estimates among the pieces of mushroom presented to the molluscs**.** The procedure used was: a) if the control weight increased, the proportional increase was added to the estimate of consumption, or b) if the control weight decreased, the proportional decrease was subtracted from the estimate of consumption. The A.I. values were then calculated using the adjusted values. The non-parametric Friedman's test (SAS ®) was used to determine if there were any significant differences among the A.I.s of the potential diets evaluated in the choice test. Acceptability indices were compared using Tukey's post hoc multiple comparison test.

### Preference for Green Plants

The objective of this experiment was to determine whether foliage of select plant species would be consumed by *P. carolinianus* when their preferred hosts were not available. No-choice tests were conducted for a selected number of 37 forest understory plant species that co-occur with *P. carolinianus* (Table 3). Some were early invading, rapidly growing species normally considered to be weeds, whereas others occurred later in plant succession. Both monocots and dicots were included. Each gypsy moth diet-reared slug was starved for 24 h prior to the initiation of the experiment and placed in a cylindrical, plastic container (9 cm diam × 4.5 cm high), lined with a single moistened paper towel. A single intact leaf of the test plant was presented to each slug with no alternative food source for a period of 24 h. A total of 30 slugs were tested per plant host. If no obvious feeding damage was observed after this period, the test plant was considered to be an unacceptable host.

## Results

### Growth

The pattern of fresh weight gain for *P. carolinianus* followed a sigmoid curve (Fig. 1a), although with considerable variation among individuals. There were significant differences among individuals in the time required to achieve reproductive maturity ($F$ = 2081.9; df = 340; $P < 0.001$),

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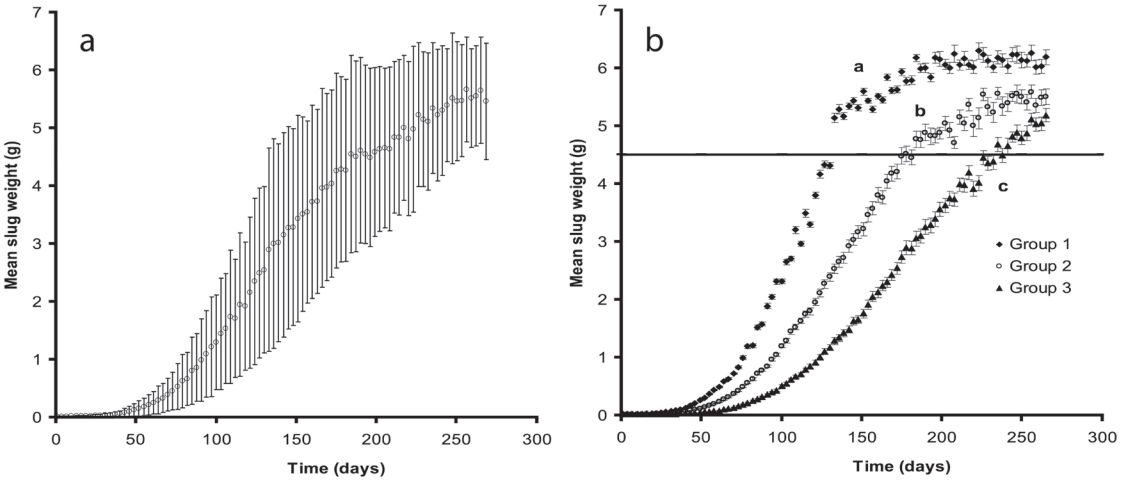



Fig. 1. Growth patterns of *P. carolinianus* slugs: (a) Mean (± SD) weight of 356 slugs reared on gypsy moth diet at 21 °C; (b) Mean weight (± SE) in 3 cohorts of slugs reared on gypsy moth diet at 21 °C. The cohorts were separated based on a hierarchical clustering analysis using date of reproductive maturity (first oviposition). The horizontal line denotes mean weight at first oviposition. Curves labeled with the same letter are not significantly different ($\alpha = 0.05$; Tukey's test).

and this was used successfully as the basis for the separation of the slugs into 4 statistically significant developmental groups (Fig. 1b).

Among the 3 groups developing successfully, 3 statistically discrete groups were observed ($F = 132.9$; df = 262; $P < 0.001$). A total of 84 slugs (24%) from the total population adhered to the growth pattern characteristic of group 1. These slugs achieved reproductive maturity in 129 ± 6 (± SD) days. The growth rate of group 1 was significantly faster than groups 2 and 3. The 79 slugs of group 2, which represented 23% of the population, achieved reproductive maturity in 173 ± 25 (± SD) days. The growth rate was significantly slower than slugs of group 1, but significantly faster than those of group 3. Group 3 took 217 ± 26 (± SD) days to attain reproductive maturity, and was represented by 102 slugs, or 30% of the test population. The mean fresh weight of individuals in all 3 groups continued to increase after first oviposition was achieved; however, the rate of weight gain progressively declined thereafter (Fig. 1b).

Group 4 was comprised of individuals that exhibited marginal mean weight gain within the first ten days, then established a trend of progressive fresh weight decline until death, and never achieving sexual maturity. Seventy-nine slugs exhibited this growth pattern, representing 23% of the test population. The mean longevity of individuals of group 4 was 37 ± 14 (± SD) days.

There were 12 individuals (of 356) that were not included in the results because they died prematurely and could not be separated into a distinct group with any level of confidence.

Longevity of *P. carolinianus* was not specifically addressed in this experiment, as the duration of evaluation was only 9 months. However, upon termination of this experiment the slugs were re-introduced to the laboratory colony and most were still alive and regularly producing eggs after 18 months of life.

There also were color changes associated with growth: there was a noticeable progressive change in the external pigmentation of *P. carolinianus* as the slugs matured. Initially, the mantle and sole of juveniles were predominantly white or cream-white, and changed to pale orange-brown as the slugs matured. The orange-brown pigmentation continued to become darker with time.

### Fecundity and Influence of Pairing

The effects of pairing on slug development varied. There was not a statistically significant difference in the length of the pre-oviposition period (juvenile stage) between solitary and paired individuals ($t = 0.98$; df = 116; $P = 0.331$) (Table 1). There also was no difference in the length of the incubation period for eggs produced by solitary versus paired slugs ($t = 1.22$; df = 205; $P = 0.225$). However, slugs reared in pairs produced significantly more eggs per clutch ($t = 3.12$; df = 228; $P = 0.002$), had a greater number of days between egg-laying events ($t = 4.15$; df = 109; $P < 0.001$), and displayed a higher proportion of successful egg hatching ($t = 4.22$; df = 228; $P < 0.001$) as compared to those reared as solitary individuals (Table 1).

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TABLE 1. COMPARISON OF REPRODUCTIVE PARAMETERS OF *PHILOMYCUS CAROLINIANUS* REARED AS INDIVIDUALS OR IN PAIRS. DATA ARE MEAN (± SE) FOR PARAMETERS LISTED.

| Reproductive parameters | Snail arrangement[a] | | Degrees of freedom | *P*-value |
|---|---|---|---|---|
| | Solitary | Pair | | |
| Pre-oviposition period (days) | 183 ± 2.7 a | 189.7 ± 8.4 a | 116 | 0.331 |
| Time between oviposition events (days) | 18.3 ± 1.1 b | 33.9 ± 2.8 a | 109 | < 0.001 |
| Number of eggs per clutch | 58.6 ± 0.7 b | 65.5 ± 2.3 a | 228 | 0.002 |
| Percent hatch | 64.7 ± 3.8 b | 84.6 ± 2.6 a | 228 | < 0.001 |
| Incubation period (days) | 21.9 ± 0.1 a | 21.6 ± 0.2 a | 205 | 0.225 |

[a]Means in rows followed by the same letter do not differ based on the 2-sample t-test ($P \leq 0.05$).

Egg production was positively correlated with egg clutch deposition order, with slightly more eggs deposited later in the sequence than earlier ($r = 0.927$; $P = 0.017$). A mean total of 58.8 ± 6.4 eggs (± SD) was produced in the first clutch whereas the number of eggs produced by the sixth clutch averaged 71.1 ± 11.1 (± SD) eggs. Percent egg hatch was not significantly correlated with oviposition sequence ($r = -0.348$; $P = 0.497$). The first clutch produced the highest mean percent hatch at 74.3 ± 34.9% (± SD) but decreased inconsistently thereafter, to 54 ± 41.9% (± SD) by the 6th clutch. Overall, the slightly increased fecundity over time was largely offset by decreased fertility.

### Temperature and Egg Development

Embryonic development occurred across the entire temperature range (10-29 °C) tested. The proportion of successful embryonic development varied significantly ($F = 10.72$; df = 174; $P < 0.001$), and was higher at 10, 14, 17 and 21 °C than at 25 and 29 °C (Fig. 2a). However, the embryos that developed at 10 and 29 °C did not hatch (Fig. 2b). All hatchlings from within a clutch that emerged successfully from the eggs, did so within 5-8 hours. Hatching success of clutches was significantly different ($F = 25.76$; df = 174; $P < 0.001$), though those incubated at 14, 17 and 21°C were not statistically different from one another, nor were those incubated at 10, 25 and 29 °C (Fig. 2b). The incubation period varied significantly among different temperature treatments ($F = 57.85$; df = 174; $P < 0.001$), decreasing with increasing temperature, so that eggs incubated at 14 °C had the longest pre-hatching period whereas those held at 25 °C the shortest (Fig. 2c).

### Suitability of Diets

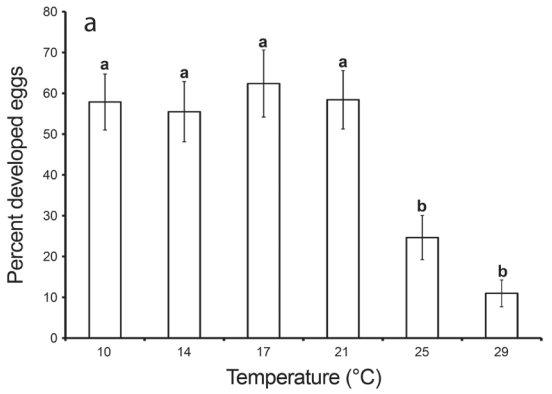
Initial weights of slugs allocated to different diet treatments did not differ ($F = 0.49$; df = 203; $P = 0.815$) (Fig. 3a). The different food sources had significant effects on the fresh weight of the slugs ($F = 92.44$; df = 153; $P < 0.001$), acting both positively and negatively (Fig. 3a). Unfed slugs had the lowest final fresh weight (1.95 g). Spruce budworm diet resulted in the highest final slug fresh weight (6.19 g), although not significantly higher than slugs fed gypsy moth diet or white mushroom. Individuals fed rabbit pellets lost the most weight over the 8-week period when compared to the other diets (other than the starvation diet), and had a final mean fresh weight of 3.31 g.

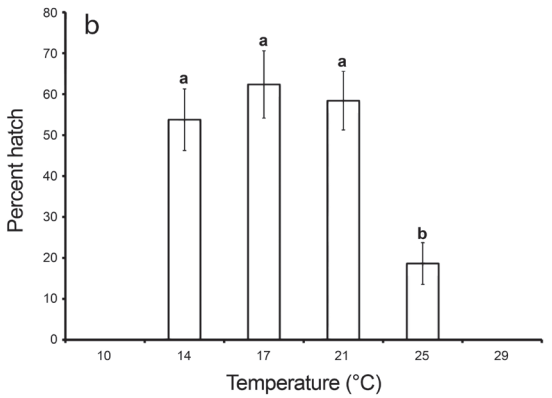
Slugs laid eggs throughout the duration of the experiment, regardless of food source. However, food source significantly ($F = 31.47$; df = 203; $P < 0.001$) affected the number of clutches produced. Slugs fed white mushroom and rabbit pellets produced, on average, less than one clutch; thus, for mushroom and rabbit pellet diets, egg production was no different than from unfed slugs (Fig. 3b). In contrast, egg production from slugs fed the other diets was equivalent, and higher than from the white mushroom, rabbit pellet, and unfed slugs. Similarly, there was significant variation in mortality associated with diet ($F = 40.81$; df = 203; $P < 0.001$), with slugs fed mushrooms and rabbit pellets having higher mortality than other groups, whereas those reared on the other diets suffered little or no mortality (Fig. 3c).

### Food Preferences

There was a significant difference ($F = 1839.61$; df = 49; $P < 0.001$) in the acceptability indexes obtained for the mushrooms and the lichen evaluated in this experiment, ranging from highly acceptable to slightly acceptable (Table 2). However, none of the mushrooms and the lichen evaluated were found to be unacceptable to *P. carolinianus*. Among the diets, 29 mushrooms and the lichen (60%) were slightly acceptable, 5 mushrooms (10%) were moderately acceptable, and 15 mushrooms (30%) were highly acceptable. There was no clear preference among the mushroom orders evaluated: Phallales and Lecanorales were not readily eaten, but there was only one representative of each order, so it is hard to draw conclusions about their relative acceptance (Table 2). Although feeding nearly indiscriminately on

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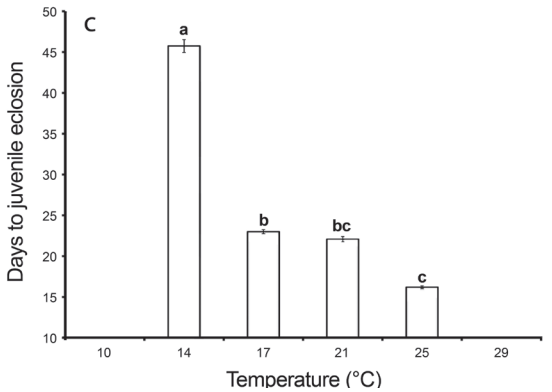
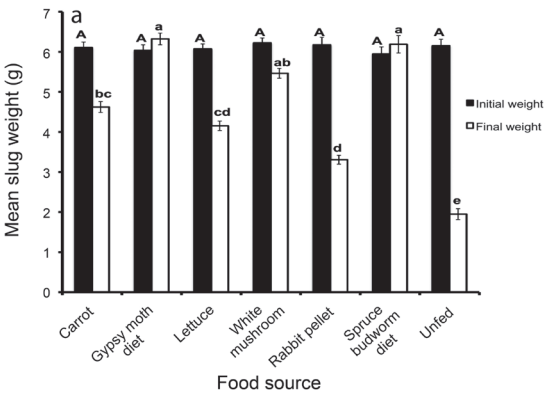
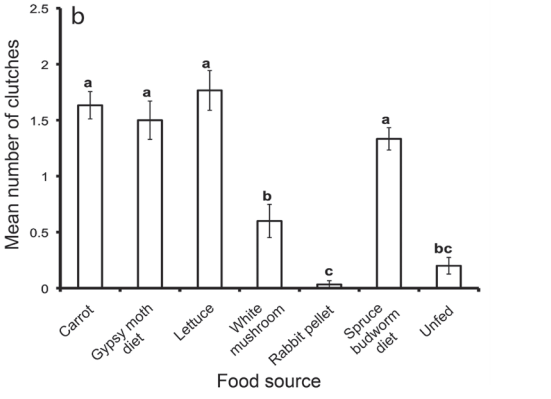




Fig. 2. Effect of temperature on *Philomycus carolinianus* eggs and hatching: (a) Mean (± SE) percent successful embryonic development of *P. carolinianus* eggs held at 6 constant temperatures. Bars with same letter are not significantly different (α = 0.05; Tukey's test); (b) Mean (± SE) percent hatch of *P. carolinianus* eggs held at 6 constant temperatures. Bars with the same letter label are not significantly different (α = 0.05; Tukey's test); (c) Mean (± SE) days to juvenile eclosion of *P. carolinianus* eggs held at 6 constant temperatures. Bars with the same letter label are not significantly different (α = 0.05; Tukey's test).



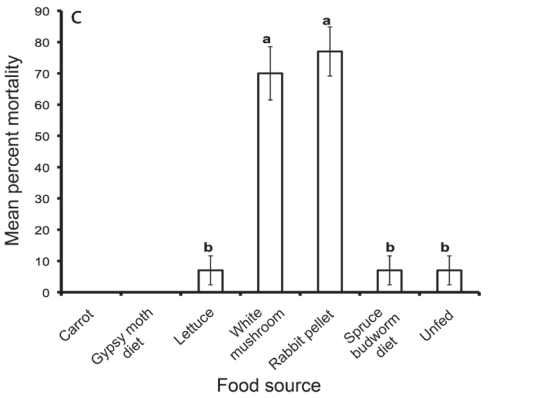




Fig. 3. Effects of diets on *P. carolinianus*: (a) Mean (± SE) weight of *P. carolinianus* slugs reared on 7 test diets for 8 weeks. Solid bars are initial weights, hollow bars are final weights. Weights followed by the same letter in the same case are not significantly different (α = 0.05; Tukey's test); (b) Mean (± SE) number of clutches produced in 8 weeks by adult *P. carolinianus* when reared on different diets. Bars with the same letter are not significantly different (α = 0.05; Tukey's test); (c) Mean (± SE) percent mortality of adult slugs of *P. carolinianus* when reared on 7 test diets for 8 weeks. Bars with the same letters are not significantly different (α = 0.05; Tukey's test).

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TABLE 2. CHOICE TEST EVALUATION OF SELECT MUSHROOM SPECIES COMMONLY FOUND IN FLORIDA FOR ACCEPTABILITY AS A FOOD SOURCE BY *PHILOMYCUS CAROLINIANUS*. VALUES SHOWN ARE ACCEPTABILITY INDEX (A.I.) OF TEST MUSHROOMS CONSUMED AS COMPARED TO THE CONTROL (WHITE MUSHROOM, *AGARICUS BISPORUS*).

| Order | Family | Species | A.I. [a,b] | Mean A.I. [a,b,c] |
|---|---|---|---|---|
| Agaricales | Agaricaceae | *Agaricus bisporus* | — | 0.42 a |
| | | *Agaricus blazei* | 0.30 op | |
| | Amanitaceae | *Amanita komarekensis* | 0.16 uv | |
| | | *Amanita phalloides* | 0.43 kl | |
| | | *Amanita rubescens* | 0.87 c | |
| | | *Amanita* sp. | 0.23 rs | |
| | | *Amanita vaginata* | 0.13 v | |
| | | *Amanita verna* | 0.25 r | |
| | | *Amanita virosa* | 0.43 kl | |
| | Auriculariaceae | *Auricularia* sp. | 0.14 v | |
| | Lepiotaceae | *Chlorophyllum molybdites* | 0.62 e | |
| | | *Leucoagaricus* sp. | 0.19 tu | |
| | | *Leucocoprinus luteus* | 0.20 st | |
| | Marasmiaceae | *Lentinula edodes* | 0.56 gh | |
| | Pluteaceae | *Pluteus* sp. | 0.41 l | |
| | Strophariaceae | *Naematoloma* sp. | 0.22 rst | |
| | Tricholomataceae | *Armillaria mellea* | 0.93 b | |
| | | *Armillaria tabescens* | 0.45 k | |
| | | *Lepista* sp. | 0.94 b | |
| | | *Collybia iocephala* | 0.57 fg | |
| | | *Macrocybe titans* | 0.33 no | |
| | Clavariaceae | prob. *Clavunopsis* sp. | 0.35 mn | |
| Phallales | Phallaceae | *Clathrus columnatus* | 0.06 w | 0.06 b |
| Lecanorales | Cladoniaceae | *Cladina evansii* | 0.04 w | 0.04 b |
| Boletales | Strobilomycetaceae | *Tylopilus felleus* | 0.15 v | 0.46 a |
| | | *Tylopilus rhoadsiae* | 0.04 w | |
| | Xerocomaceae | *Phylloporus boletinoides* | 0.99 a | |
| | Sclerodermataceae | *Scleroderma* sp. | 0.53 hi | |
| | Suillaceae | *Suillus cothurnatus* | 0.60 ef | |
| | Boletaceae | *Boletus edulis* | 0.05 w | |
| | | *Boletus granulosiceps* | 0.29 pq | |
| | | *Boletus luridiceps* | 0.99 a | |
| | | *Boletus oliveisporus* | 0.92 b | |
| | | *Boletus ornatipes* | 0.57 fg | |
| | | *Boletus rubellus* | 0.42 kl | |
| | | *Boletus underwoodii* | 0.33 no | |
| | | *Leccinum albellum* | 0.14 v | |
| Cantharellales | Hydnaceae | *Hydnum* sp. | 0.13 v | 0.47 a |
| | Cantharellaceae | *Cantharellus cibarius* | 0.82 d | |
| Polyporales | Ganodermataceae | *Ganoderma applanatum* | 0.51 ij | 0.47 a |
| | | *Ganoderma lucidum* | 0.55 gh | |
| | | *Ganoderma* sp. | 0.26 qr | |
| | Polyporaceae | *Lentinus crinitus* | 0.37 m | |
| | | *Lentinus* sp. | 0.83 d | |
| | | *Panus rudis* | 0.49 j | |
| | | *Trametes* sp. | 0.44 kl | |
| | | *Tyromyces* sp. | 0.32 nop | |
| | Pleurotaceae | *Pleurotus ostreatus* | 0.42 kl | |
| Russulales | Russulaceae | *Lactarius hygrophoroides* | 0.63 e | 0.56 a |
| | | *Lactarius luteolus* | 0.25 r | |

[a]Values within each column followed by the same letter are not significantly different by Tukey's multiple comparison test ($P < 0.05$).
[b]Higher values indicate greater acceptance of the test mushroom.
[c]Mean A.I. is the average for mushrooms in the respective orders.

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fungi, *P. carolinianus* did not feed on any of the forest understory or weedy plant species evaluated (Table 3).

## Discussion

### Growth

*Phylomycus carolinianus* specimens held at 21 °C generally displayed incremental growth for the first 50 days, followed by rapid weight gain, then a reduced rate of growth after approximately 200 days (Fig. 1a). There were large variations in rate of weight gain among slugs, both within and among clutches, which are not completely evident in the growth curve based solely on averages. As noted by Zotin (2007), average growth curves derived from multiple specimens mask individual growth patterns. Because of this variation, the time to reproductive maturity was selected as the basis for separating slugs into distinct groups of individuals displaying disparate rates of weight gain. Four discrete growth patterns were exhibited by *P. carolinianus*: under laboratory conditions groups 1, 2, and 3 had dissimilar rates of weight gain to reproductive maturity (Fig. 1b), whereas group 4 had progressive reduction in weight until death.

Table 3. Green plants used to assess plant consumption in no-choice tests.

| Weedy plants | Forest understory plants |
|---|---|
| *1.* Monocotyledons | |
| *Commelina diffusa* | *Panicum dichotomiflorum* |
| *Cyperus brevifolius* | *Microstegium vimineum* |
| *Cyperus globulosus* | *Digitaria ciliaris* |
| *Cyperus rotundatus* | |
| *Andropogon virginicus* | |
| *Digitaria sanguinalis* | |
| *Eleusine indica* | |
| *2.* Dicotyledons | |
| *Alternanthera pungens* | *Lespedeza striata* |
| *Bidens alba* | *Callicarpa americana* |
| *Drymaria cordata* | *Vitis* sp. |
| *Ambrosia artemisiifolia* | *Smilax bona-nox* |
| *Eupatorium capillifolium* | *Smilax rotundifolia* |
| *Wedelia trilobata* | *Smilax glauca* |
| *Dichondra carolinensis* | *Diospyros* sp. |
| *Chamaesyce hirta* | *Galium aparine* |
| *Phyllanthus urinaria* | *Desmodium tortuosum* |
| *Portulaca amilis* | *Hedyotis corymbosa* |
| *Portulaca oleracea* | *Rubus cuneifolius* |
| *Richardia brasiliensis* | *Acalypha* sp. |
| *Hydrocotyle* sp. | *Nephrolepis* sp. |
| *Arachis glabrata* | |

The high degree of variability in growth rate suggests the evolution of risk-spreading (bet-hedging) (Hopper 1999; Wilbur & Rudolf 2006; Simons 2011). Many organisms inhabiting uncertain environments display varying degrees of developmental delay and reproductive delay (Simons 2011). One explanation is genetically predetermined staggering of growth to reduce sibling competition for a limited resource. Another could be a survival mechanism to increase the probability of host location by some offspring when food resources are inconsistent. The latter seems especially appealing given the ephemeral nature of food for fungus-feeding organisms. It is difficult to think of an explanation for the existence of group 4, as these represent developmental failures. There was no indication that these were trophic eggs, as such eggs usually are infertile and the group 4 eggs hatched successfully. It is possible that group 4 eggs are the last to be deposited from each clutch and are endowed with fewer biological resources for survival. Documenting the order in which the eggs are oviposited for each clutch, then statistically determining whether there is a correlation between the order in oviposition and growth rate, could test this hypothesis. Certainly the last-laid eggs tend to be smaller, though only the last few eggs in each clutch are noticeably smaller.

### Fecundity and Influence of Pairing

Hermaphroditism is common among terrestrial slugs (Jarne & Auld 2006), though hermaphroditic molluscs may display outcrossing, inbreeding (self-fertilization or selfing) or mixed mating systems (variation within or among populations (Jarne & Charlesworth 1993). This experiment showed that *P. carolinianus* is capable of selfing. Interestingly, the reproductive outputs of selfed *P. carolinianus* appeared to be comparable to paired individuals. Though paired slugs produced clutch sizes slightly larger than individual slugs, and clutches from paired slugs displayed a higher mean percent hatch, the fecundity and fertility benefits of pairing seem to be offset by the more frequent egg production among solitary (selfed) slugs. For example, during a 2-month period, the shorter 18.3-day interval between clutches for solitary slugs potentially allows them to have 3 generations, whereas the 33-day interval of paired slugs allows them to have only 2 generations. Assuming no mortality and consistent fecundity and fertility rates, the solitary individuals will produce far more offspring than will paired slugs within this 2-month period. This differential reproductive rate may account for the persistence of selfing in these animals. Although in the short-term (a single generation) there was no significant disadvantage to self-fertilization, deleterious effects might accumulate over multiple generations of self-fertilization.

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*Philomycus carolinianus* was not previously known to be capable of reproducing by self-fertilization (Anderson & McCracken 1986; McCracken & Selander 1980). Anderson & McCracken (1986) concluded that although hermaphroditic slugs have been thought to self-fertilize infrequently, it was more commonplace than thought. Nevertheless, based on electrophoretic studies of genetic variation they concluded that *P. carolinianus* reproduced primarily by out-crossing. They also noted that there was some level of genetic homogeneity within populations, which they attributed to sampling error and inbreeding. However, self-fertilization can also lead to high genetic homogeneity. How *P. carolinianus* reproduces in nature is open to debate, but clearly they are capable of self-fertilization, do not seem to display a reproductive penalty for not outcrossing, and in terms of simple reproductive output may even benefit from selfing. As noted previously, reproduction by hermaphroditic animals is not always consistent. For example, Foltz et al. (1982) found both heterozygous and monogenic strains among some species of arionid slugs, apparently indicating both out-crossing and selfing populations within the same species.

It was not certain in this experiment whether paired specimens reproduced by self-fertilization or cross-fertilization. We observed elaborate mating rituals among paired individuals wherein both individuals exhibited trail-following, followed by the pressing together of the anterior regions, as described by Webb (1968). However, this anecdotal evidence for mating was not confirmed by dissection, as was performed by Webb (1968), who described reciprocal insemination.

### Temperature and Egg Development

Temperature influences biological parameters of all living organisms, though the extensive geographical distribution of *P. carolinianus* (ranging from temperate to subtropical regions of North America) suggests broad tolerance for temperatures (Hubricht 1985; Pilsbry 1948). Indeed, the results of this experiment suggest that embryonic development (as here defined) of *P. carolinianus* eggs can occur across the entire temperature range tested, between 10 and 29 °C. However, the proportion of embryos completing development successfully declined above 21 °C, with eggs held at 25 and 29 °C displaying significantly reduced embryonic development (Fig. 2a). This implies a distinct seasonality to reproduction, and some latitudinal constraints on distribution at both high and low latitudes.

Evaluation of hatching success indicated that the optimal temperature range for *P. carolinianus* was somewhere between 10 and 25 °C, but certainly between 14 and 21 °C. Low hatching success occurred in eggs held at 25 °C, and eggs held at 10 and 29 °C did not hatch (Fig. 2b). The 29 °C constant temperature appeared to exceed the upper temperature development threshold for *P. carolinianus* eggs, as embryos that developed appeared to be viable only for a brief period and did not hatch. Similarly, although 57% of *P. carolinianus* eggs held at 10 °C exhibited embryonic development, none hatched after 100 days of observation (Fig. 2c). On the 120th day of observation, a total of 5 clutches (267 eggs) that had been held at the 10 °C temperature were randomly selected and removed. These eggs were placed on a laboratory counter overnight (~ 18h) at an ambient temperature of approximately 22 °C. The next morning, all (100%) the eggs that had previously displayed embryonic development hatched. The mean proportion of juveniles that hatched was calculated for all 5 clutches, yielding a mean value of 63.0 ± 12%. None of the eggs that remained at the 10 °C treatment temperature hatched during the prescribed period of evaluation (180 d). After 180 days, the eggs were placed on the laboratory counter at the ambient temperature described previously and held for 2 weeks. The eggs rapidly deteriorated and there was no eclosion.

*Philomycus carolinianus* eggs can survive extended periods of low temperatures, suggesting that eggs could serve as an over-wintering stage. Supporting this, it is evident that embryonic development proceeds at low temperatures and viable embryos will persist for extended periods and emerge when environmental conditions improve. Although constant temperatures used in laboratory evaluations are not a feature of natural environments, the pre- and post-eclosion development trends of *P. carolinianus* observed in this experiment could form a useful basis on which to make inferences about similar phenomena in natural populations.

### Suitability of Diets

Suitability of the diets that were evaluated varied greatly, with white mushroom, gypsy moth, and spruce budworm diets producing the greatest slug weights, suggesting superior suitability as slug food. Slugs reared on these 3 diets consistently laid eggs throughout the duration of the experiment; however, mortality was very high for slugs fed white mushroom, and egg production was lower. The quality of the white mushroom inside each container degraded rapidly and may have been responsible for the higher mortality in this diet treatment. Post-experiment, when the mushroom was replaced and rearing containers changed with greater frequency, the mortality rate was substantially reduced. This suggests that low quality of white mushroom as a possible food source may be an artifact of the experimental protocol. The gypsy moth and spruce budworm insect diets remained palatable to the slugs for the

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longest periods. This is likely due to the antibiotic (preservative) compounds included in the formulations. The success that we had in culturing these animals on insect diets suggests that this approach could provide easy, reliable, economical means of studying the biology of this and related slugs without the necessity of acquiring natural foods.

Carrot and lettuce could be considered to be reasonable alternatives to white mushroom, gypsy moth, and spruce budworm diets. Fresh weights of individuals reared on carrot and lettuce were lower, but these slugs produced large numbers of clutches with low percent mortality among the slugs. The least suitable diet was rabbit pellets. There was substantial weight loss of slugs reared on this diet, these animals produced only a single clutch, and the slugs experienced high mortality. This food source also was rapidly colonized by saprophytic fungi and bacteria. Interestingly, Rueda (1989) found rabbit pellets to be a superior diet for *Sarasinsula plebia* (Fischer, 1868), though this slug is phytophagous rather than fungivorous.

Upon the termination of this trial, all slugs surviving from the unfed treatment were reintegrated into the laboratory colony and maintained on gypsy moth diet. These slugs rapidly gained weight and in approximately 3 weeks had achieved mean weights comparable to specimens of similar age that had been maintained continuously on gypsy moth diet. Also, these slugs produced clutches with similar frequency and of similar mean clutch size as slugs maintained in the colony. This suggests that populations in natural habitats could endure prolonged food deprivation, and quickly recover when conditions improved. Martin & Bergey (2013) similarly reported the ability of food-deprived, stunted snails to recover when provided adequate food, catching up to the non-stunted snails.

### Food Preferences

The diet of *P. carolinianus* has been reported to consist of a wide variety of mushrooms, with little noticeable species preference under natural conditions (Ingram 1949). The results of this experiment confirm that this species feeds on a broad range of fungi. Although none of the mushroom species presented to this animal was rejected, it was clear that *P. carolinianus* displayed some preferences under laboratory conditions; in particular, slugs displayed significant differences in preference among genera and species.

Several species of understory plants were offered to *P. carolinianus*; however, none were consumed, suggesting that despite the ability to feed on Romaine lettuce under laboratory conditions, this species will not likely consume green plant material in natural habitats. However, his might warrant further study using slugs that were not cultured on artificial diets.

In summary, *P. carolinianus* demonstrated 4 distinct growth patterns under laboratory conditions, possibly a bet-hedging adaptation to varying availability of transient food supplies. Crossmating is not required; this slug has the ability to reproduce by self-fertilization**.** It is not certain, however, what degree of self-fertilization occurs in nature. Clutch sizes produced by this slug can be as large as 102 eggs, with percent hatch approaching 100%. Eggs can develop and hatch over a wide temperature range. *P. carolinianus* will consume many mushroom species and can survive for at least 8 weeks without food, with full recovery when favorable conditions return. Green plants seem not to be a normal part of this slug's diet. *P. carolinianus* is irrefutably a resilient species, and the attributes investigated in this study may contribute to the ability of this species to successfully colonize much of North America.

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