GROWTH PLASTICITY WITH CHANGING DIET IN THE LAND
SNAIL *PATERA APPRESSA* (POLYGYRIDAE)

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ABSTRACT

Diets of most snail species are unstudied, but the diets of non-native snails are of special interest because these species may be pests or compete with native species. We tested whether the apparent leaf-litter diet of a colony of the non-native land snail *Patera appressa* from a plant nursery was adequate to support growth, and whether growth rate could be altered by changing diet. Growth was tested in two laboratory experiments using combinations of leaf litter and live plant matter (romaine lettuce). In the first experiment, snails were given a diet of litter, lettuce or both. In the second experiment, the snails from the first experiment were all given both litter and lettuce, and additional colony snails were given only litter (i.e. loss of lettuce). Snails showed rapid growth with live plant material and stunted growth on a diet of only leaf litter, indicating that leaf litter alone is not a good diet and that the snails are likely consuming live plants at the nursery. Changing the diet revealed growth plasticity. The addition of live plant material reversed the previously stunted growth on a litter-only diet, and the stunted snails caught up in size with non-stunted snails. Under conditions of changing food resources, growth plasticity enables large size at maturity, which likely has fitness consequences.

INTRODUCTION

The ecological niche of most non-native land snails and slugs is inadequately known (Paustian & Barbosa, 2012), including information on species-specific snail diets and the effects of food quality. Because snails commonly eat decaying vegetation, non-native snails may cause little, if any, noticeable impacts. Exceptions include snails that have become pests or that are non-selective predators (e.g. Griffiths, Cook & Wells, 1993; Cowie, 2001; Raut & Barker, 2002; Cowie et al., 2009).

The horticultural trade is a common route of long-distance dispersal for snails, and the consequent establishment of snails in plant nurseries is a result and contributing factor in this dispersal. Indeed, many nurseries support populations of non-native snails (E. A. Bergey, unpubl.; Cowie, et al., 2008) and some of these species can be nursery pests. Examples include *Zonitoides arboreus* in Hawaii, where this species damages exposed roots in orchids (Hollingsworth & Armstrong, 2003) and many species of European slugs. Often, however, nursery-dwelling snails do not produce noticeable plant damage and are not considered pests.

*Patera appressa* (Say, 1821), the flat bladetooth (Polygyridae), is a recently reported snail in Oklahoma plant nurseries (Bergey, unpubl.). The species is native to the southeastern United States, east of the Mississippi River (Burch, 1962; Hubricht, 1985), and colonies have been found outside its native range in Indiana (Webb, 1942) and Maryland (Jackson, 1950; Grimm, 1959). *Patera appressa* is found in various habitats, including stony embankments and urban areas (Branson & Batch, 1988; Hubricht, 1985). We found a large, established population in a plant nursery in Norman, Oklahoma, c. 1050 km out of the species’ native range. Snails were abundant in outside areas in and under up-ended large ceramic pots on gravel and wood mulch and in unkempt areas, and were rare inside greenhouses. Although locally abundant in some areas of the nursery, the snails were not considered a plant pest by the nursery manager.

Our study had two objectives. The first objective was to determine whether the apparent food source of *P. appressa* at the greenhouse—leaf litter—was adequate to support snail growth. The second objective was an offshoot of the first; namely, if growth was slowed by an inadequate diet, would snails respond to diet supplementation? Thus, we were interested in both a situation-specific question (was *P. appressa* consuming live plant material or was leaf litter alone an adequate diet?) and a more general question on snail growth (can growth rate vary with changing diets?). Although diet can affect growth rates and adult size, we have seen no studies of the effects of changing diets during land snail growth.

METHODS

Material and experimental design

We ran two laboratory growth experiments using young snails in the first generation of a colony of *Patera appressa* that was sourced...
from a plant nursery in Norman, Oklahoma. The colony was fed lettuce and leaf litter, supplemented with powdered calcium carbonate. Both experiments used the same experimental design. Snails were reared in tall plastic petri dishes (8.5 cm wide and 2.5 cm deep) with aeration holes in the lids. Each petri dish had a 1-cm layer of potting soil. Each diet treatment had five replicates with three snails each. Individual snails within a petri dish were marked with one dot of acrylic paint (red, yellow or blue) close to the shell aperture, so that snails could be differentiated. Snails were photographed with a Wild M5 dissecting microscope fitted with a SPOT Idea camera (Diagnostic Instruments; Sterling Heights, MI, USA) and shell diameter was measured using an ocular micrometer at 8× magnification at the start of an experiment and bi-weekly during experiments. Experiments lasted about 8 weeks. Snails were fed various combinations of romaine lettuce and partially decomposed leaf litter (primarily from oak, maple and sycamore leaves) and all dishes were sprinkled with powdered calcium carbonate. Petri dishes were checked every 3 d, and fresh lettuce was added and dishes were sprinkled with spring water to maintain moisture, as needed.

The first experiment (Experiment 1) was designed to indicate whether young *P. appressa* grew well with a diet of leaf litter, the apparent diet of adult snails. We followed snail growth under three different diets: only leaf litter, leaf litter supplemented with lettuce, and only lettuce. Forty-five, 2-week-old snails were marked, measured, photographed and distributed among 15 petri dishes. This growth experiment ran from 2 May to 27 June 2012.

We designed the second experiment based on the observations and bi-weekly data obtained during the first experiment. Growth diverged among treatments and we wanted to determine whether the growth rate of snails would change if diet were changed. At the end of Experiment 1 on 27 June, treatments were altered so that all of the three diet treatments from Experiment 1 became leaf litter and lettuce; that is, lettuce was added to the leaf litter treatment, leaf litter was added to the lettuce treatment, and the leaf litter and lettuce treatment was unchanged. In addition to these three treatments, a fourth treatment was added using colony snails from the same cohort used in the first experiment. These colony snails had been reared on both leaf litter and lettuce and, when added to the experiment (five replicates of three marked snails each), were given only leaf litter (i.e. loss of lettuce). Experiment 2 ran from 27 June to 29 August 2012.

### Data analysis

Shell diameters of the three snails in each petri dish were averaged. This produced five replicates for each treatment in Experiments 1 and 2. Data were analysed in two forms, size data and growth curves. The size data were initial size, final size and growth. Growth was the final mean size minus the initial mean size for each replicate.

The size data were analysed using the nonparametric Kruskall-Wallis test with either three treatments (Experiment 1) or four treatments (Experiment 2) using Statview software (SAS, v. 5.0.1). For significant Kruskall-Wallis tests, significantly different treatments were identified using a nonparametric multiple-comparisons test (Zar, 1996).

Growth curves (the rate of growth over the experiment) were analysed using the CompareGrowthCurves module from Statmod, a statistical modeling package based on R (Smyth, 2006), using 10,000 permutations.

### RESULTS

**Experiment 1: is leaf litter an adequate diet?**

At the start of Experiment 1, there was no statistical difference in snail size among the three diet treatments (Kruskal-Wallis, $H = 5.173, P = 0.07$; Fig. 1). Mean shell diameter was 4.06 mm (SE = 0.23). Final shell diameter on day 56 differed among treatments (Fig. 2A; Kruskal-Wallis, $H = 10.8, P = 0.004$). Snails fed leaf litter were significantly smaller than the snails fed both leaf litter and lettuce (Tukey’s test, $P < 0.05$). Snails fed only lettuce were intermediate in size. Snails fed only leaf litter grew much less than snails fed both leaf litter and lettuce and snails fed only lettuce (Fig. 2B; Kruskal-Wallis, $H = 9.28, P = 0.01$).

Growth curves were nearly linear for all diet treatments (Fig. 1). The growth curves for lettuce-fed and both litter- and lettuce-fed snails did not differ (statistic = −0.85, $P = 0.39$);
however, the growth curve of litter-fed snails differed significantly from that of snails fed both litter and lettuce (statistic $= -4.25$, $P = 0.007$) and snails fed lettuce (statistic $= -8.364$, $P = 0.007$).

**Experiment 2: diet augmentation**

At the start of Experiment 2, the snails from the four treatment groups were significantly different in shell diameter (Kruskal-Wallis; $H = 14.791$, $P = 0.002$; Fig. 3A). Snails previously fed leaf litter were significantly smaller than snails fed both litter and lettuce. Snails previously fed lettuce and snails from the colony (fed both litter and lettuce) were intermediate in shell diameter.

Final shell diameters of the three sets of snails fed both leaf litter and lettuce were not significantly different (Fig. 3B); however, the snails from the colony, which were fed only leaf litter, were significantly smaller (Kruskal-Wallis; $H = 15.526$, $P = 0.0014$). The colony treatment snails started in the middle size range but were the smallest in size by the end of the experiment. At the end of the experiment, many of the snails were forming a reflexed lip at the shell aperture, which signifies the end of shell growth and attainment of maximum shell size. However, none of the smaller litter-fed snails from the colony were forming a lip.

Snails from the colony only fed leaf litter grew significantly less than the snails from Experiment 1 fed litter supplemented with lettuce (Kruskal-Wallis; $H = 16.155$, $P = 0.0011$; Fig. 3C). Growth of snails fed lettuce augmented with litter, and snails continuously fed both litter and lettuce, had intermediate growth.

Growth curves for the three treatments of snails from Experiment 1 started the experiment at different sizes and converged in size as the experiment progressed (Fig. 4). In contrast, the growth curve for colony snails fed only litter was relatively flat. Statistically, the growth curves for snails continuously fed both leaf litter and lettuce, and snails fed lettuce augmented with litter, did not differ (statistic $= -2.57$, $P = 0.075$), whereas all other growth curves differed from each other (absolute values of statistic range: 2.81–10.10; $P = 0.007–0.008$).

**DISCUSSION**

Our results indicate that the growth rate of *Patera appressa* is strongly affected by diet and that a diet restricted to decaying leaf litter reduces growth rates in comparison to a diet that also includes live plant material. Snails may preferentially consume plants with higher nutrients (Iglesias & Castillejo, 1999, but see Speiser & Rowell-Rahier, 1991) and the readily consumed romaine lettuce provided water, calcium, protein, sodium, potassium and other nutrients (U.S. Department of Agriculture, 2012). In a study with defined diets in an agar matrix, Wacker & Baur (2004) found that protein level positively influenced shell growth and final size of the snail *Arianta arbustorum*. Calcium may influence growth (but see Wacker & Baur, 2004) and low calcium may reduce survival (Wacker & Baur, 2004).

Many land snails in the wild eat a diet consisting primarily of detritus and decaying vegetation (Richardson, 1975; Williamson & Cameron, 1976; Hatzioannou, Eleutheriadis & Lazaridou-Dimitriadou, 1994; Mensink & Henry, 2011; Schamp, Horsák & Hájek, 2010). *Patera appressa* was common in a plant nursery area with no noticeable green plants (i.e. snails were found primarily...
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among statutory and pots resting on gravel with scattered mulch). The consequent conclusion that this species is primarily a detritivore was not supported by the stunted growth on a leaf litter diet and increased growth when the diet included green plants. Although we found that green plants increased growth, Williamson & Cameron (1976) reported that various diets that included plants in laboratory-reared Cepaea nemoralis produced slower growth than in a field population, indicating an incomplete diet. Indeed, many detritivorous snails and slugs may be unapparent opportunistic feeders, consuming some live plant material (as suggested in this study), soil and humus (Williamson & Cameron, 1976), and possibly even animal matter (e.g. Iglesias & Castillejo, 1999; Barker & Elford, 2004; Dourson, 2008). Alternatively, juveniles may eat more live plant material than adults (Iglesias & Castillejo, 1999), so that supplementation with green plants may produce better growth of young snails, but effects may be less apparent in adults—the stage found at the nursery.

Patera appressa is not native to Oklahoma and the greenhouse location was the first record of this species in the state. The snails successfully overwintered (as did a non-native population in Indiana; Webb, 1942) and maintained a population over the hot, dry summer. We subsequently found the species in other nurseries (Bergey, unpubl.) and in Oliver’s Woods Ecological Laboratory and Natural Area (J. Kurien, unpubl.), which is located about 2 km from the plant nursery site. Oliver’s Woods has a diverse snail assemblage and it is not known whether P. appressa competes with native snail species. In a study of three co-occurring slug species, Paustian & Barbosa (2012) demonstrated that the diet of non-native species partially overlapped that of one of the native slugs, but concluded that microhabitat differences resulted in little or no competition.

Plasticity in growth occurred when the snails alternated between diets of different quality. Snails raised on a poor diet (leaf litter) were able to catch up in growth when their diet was supplemented with live plant material, and snail growth was stunted when live plant material was removed. The ability to change growth rates may allow individuals to maximize growth when a higher quality or greater quantity of food is available. Rapid growth may allow snails to escape predation if they are too large for predators to handle (Baur, 1990). If adult size is affected, maximizing growth will affect fitness, as larger snails can produce more (Baur, 1988; Anderson, Weaver & Guralnick, 2007) and/or larger eggs than smaller conspecifics. Baur (1990) similarly found that egg cannibalism increased growth of juveniles, but that adult size was not affected. In addition to diet, snail size can be influenced by altitude, temperature, moisture and population density (Dan & Bailey, 1982; Goodfriend, 1986; Baur, 1988; Jess & Marks, 1995; Anderson et al., 2002) and by variation among individuals (Hanley, Bulling & Fenner, 2003; Beeby & Richmond, 2007).

In conclusion, our study indicated that some land snails that are assumed to be detritivores may have a wider diet and participate as consumers and even predators in food webs. Additionally, plasticity in growth allows land snails to maximize growth under changing environmental conditions.

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