Journal of
Molluscan Studies

The Malacological Society of London

Journal of Molluscan Studies (2013) **79**: 364–368. doi:10.1093/mollus/eyt033
Advance Access publication date: 2 October 2013

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

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(Received 9 February 2013; accepted 20 August 2013)

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. All petri dishes 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 Images; 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, *c.* 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, $H = 9.28$, $P = 0.01$).

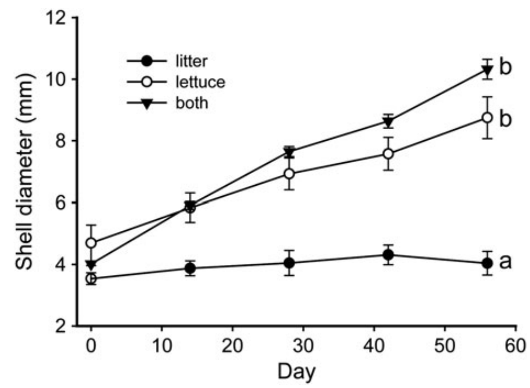

Figure 1. Growth in shell diameter with different diets in *Patera appressa*. Growth curves are from diets of aged leaf litter, romaine lettuce, and both leaf litter and lettuce. Bars show ±1 SE and different letters next to lines show significant differences among growth rate lines.

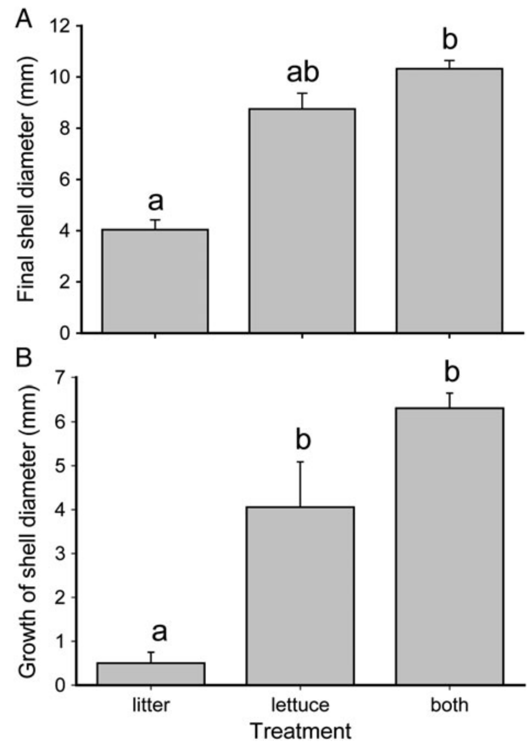

Figure 2. Change in shell size with different diets in *Patera appressa* in terms of shell size at the end of Experiment 1 (**A**) and growth of the shell during the experiment (**B**). Diets were aged leaf litter, romaine lettuce and both leaf litter and lettuce. Bars show +1 SE and different letters over bars show significant differences among diets.

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, $P = 0.39$);

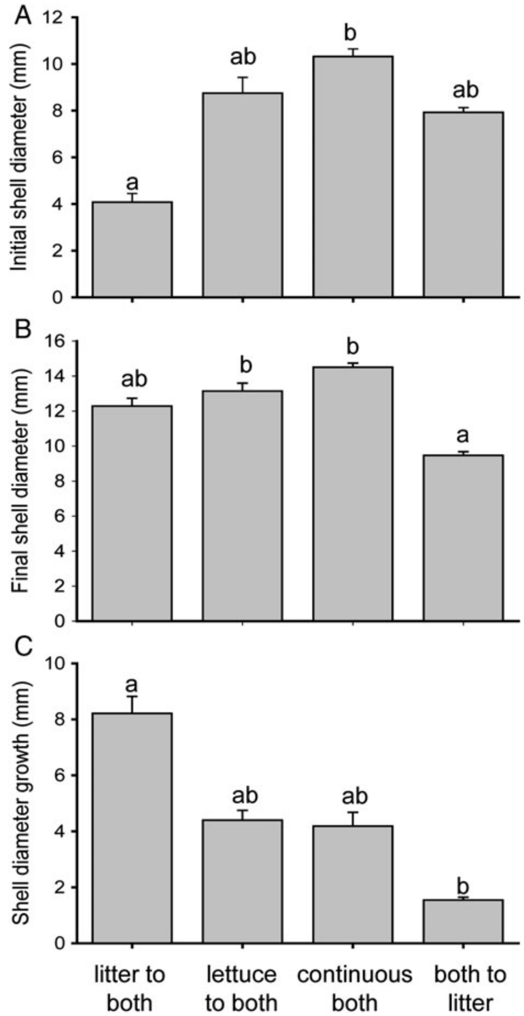

Figure 3. Effect of different diets on snail shell size. **A.** Initial shell diameter at the beginning of Experiment 2. **B.** Final shell diameter at the end of Experiment 2. **C.** Growth of the shell during Experiment 2. Diets were: 'litter to both' (fed litter in Experiment 1 and fed both litter and lettuce in Experiment 2); 'lettuce to both' (fed romaine lettuce in Experiment 1, then fed both litter and lettuce in Experiment 2); 'continuous both' (fed leaf litter and romaine lettuce in Experiments 1 and 2); 'both to litter' (colony snails formerly fed on a diet of leaf litter and lettuce and then fed only litter in Experiment 2). Bars show +1 SE and different letters over bars show significant differences among diets.

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.

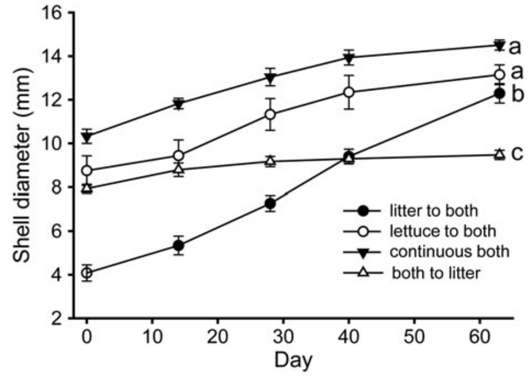

Figure 4. Growth in shell diameter after dietary changes in *Patera appressa*. The growth curves show shell growth of snails from the end of Experiment 1 (fed litter, lettuce, or both litter and lettuce), which were fed both litter and lettuce during this experiment ('litter to both', 'lettuce to both', and 'continuous both'; respectively), as well as additional colony snails (reared on litter and lettuce) that were fed litter only ('both to litter'). Bars show ±1 SE and different letters next to lines show significant differences among growth lines.

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 = −2.37; $P = 0.075$), 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; Hatziioannou, 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 among statuary 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 & Efford, 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*., 2007) 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.

ACKNOWLEDGEMENTS

Eric Ray, Jobin Kurien, Lisa Price and Dr Mike Mather helped collect snails for the colony and Mike Mather identified the snails. Funding was provided by a University of Oklahoma Undergraduate Research Opportunities Program grant to R.M. and an Oklahoma Biological Survey grant to E.A.B.

REFERENCES

ANDERSON, T.K., WEAVER, K.F. & GURALNICK, R.P. 2007. Variation in adult shell morphology and life-history traits in the land snail *Oreohelix cooperi* in relation to biotic and abiotic factors. *Journal of Molluscan Studies*, **73**: 129–137.

BARKER, G.M. & EFFORD, M.G. 2004. Predatory gastropods as natural enemies of terrestrial gastropods and other invertebrates. In: *Natural enemies of terrestrial molluscs* (G.M. Barker, ed.), pp. 279–403. CABI Publishing, Wallingford, UK.

BAUR, B. 1988. Population regulation in the land snail *Arianta arbustorum*: density effects on adult size, clutch size and incidence of egg cannibalism. *Oecologia*, **77**: 390–394.

BAUR, B. 1990. Possible benefits of egg cannibalism in the land snail *Arianta arbustorum* (L.). *Functional Ecology*, **3**: 679–684.

BEEBY, A. & RICHMOND, L. 2007. Differential growth rates and calcium-allocation strategies in the garden snail *Cantareus aspersus*. *Journal of Molluscan Studies*, **73**: 105–112.

BRANSON, B. & BATCH, D. 1988. Distribution of Kentucky land snails (Mollusca: Gastropoda). *Transactions of Kentucky Academy of Science*, **49**: 101–116.

BURCH, J.B. 1962. *How to know the eastern land snails*. W.C. Brown, Dubuque, IA.

COWIE, R.H. 2001. Invertebrate invasions on Pacific Islands and the replacement of unique native faunas: a synthesis of the land and freshwater snails. *Biological Invasions*, **3**: 119–136.

COWIE, R.H., DILLON, R.T., ROBINSON, D.G. & SMITH, J.W. 2009. Alien non-marine snails and slugs of priority quarantine importance in the United States: a preliminary risk assessment. *American Malacological Bulletin*, **27**: 113–132.

COWIE, R.H., HAYES, K.A., TRAN, C.T. & MEYER, W.M. 2008. The horticultural industry as a vector of alien snails and slugs: widespread invasions in Hawaii. *International Journal of Pest Management*, **54**: 267–276.

DAN, N. & BAILEY, S. 1982. Growth, mortality, and feeding rates of rates of the snail *Helix aspersa* at different population densities in the laboratory, and depression of activity of helicid snails by other individuals, or their mucus. *Journal of Molluscan Studies*, **48**: 257–265.

DOURSON, D.C. 2008. The feeding behavior and diet of an endemic West Virginia land snail, *Triodopsis platysayoides*. *American Malacological Bulletin*, **26**: 153–159.

GOODFRIEND, G.A. 1986. Variation in land-snail shell form and size and its causes: a review. *Systematic Biology*, **35**: 204–223.

GRIFFITHS, O., COOK, A. & WELLS, S.M. 1993. The diet of the introduced carnivorous snail *Euglandina rosea* in Mauritius and its implications for threatened island gastropod faunas. *Journal of Zoology*, **229**: 79–89.

GRIMM, W. 1959. Land snails from Maryland and Virginia. *Nautilus*, **73**: 21–22.

HANLEY, M., BULLING, M. & FENNER, M. 2003. Quantifying individual feeding variability: implications for mollusc feeding experiments. *Functional Ecology*, **17**: 673–679.

HATZIIOANNOU, M., ELEUTHERIADIS, N. & LAZARIDOU-DIMITRIADOU, M. 1994. Food preferences and dietary overlap by terrestrial snails in Logos Area (Edessa, Macedonia, Northern Greece). *Journal of Molluscan Studies*, **60**: 331–341.

HOLLINGSWORTH, R. & ARMSTRONG, J. 2003. Effectiveness of products containing metaldehyde, copper or extracts of yucca or neem for control of *Zonitoides arboreus* (Say), a snail pest of orchid roots in Hawaii. *International Journal of Pest Management*, **49**: 115–122.

HUBRICHT, L. 1985. The distributions of the native land mollusks of the eastern United States. *Fieldiana: Zoology, New Series*, **24**: 1–191.

IGLESIAS, J. & CASTILLEJO, J. 1999. Field observations on feeding of the land snail *Helix aspersa* Müller. *Journal of Molluscan Studies*, **65**: 411–423.

JACKSON, R.W. 1950. *Mesodon appressus* form *sculptior* Chadwick in Maryland. *Nautilus*, **64**: 67.

JESS, S. & MARKS, R.J. 1995. Population density effects on growth in culture of the edible snail *Helix aspersa* var. *maxima*. *Journal of Molluscan Studies*, **61**: 313–323.

MENSINK, P.J. & HENRY, H.A.L. 2011. Rain events influence short-term feeding preferences in the snail *Cepaea nemoralis*. *Journal of Molluscan Studies*, **77**: 241–247.

PAUSTIAN, M.E. & BARBOSA, P. 2012. Overlap of food and microhabitat preferences among some native and nonnative slugs in mid-Atlantic forests of eastern North America. *Journal of Molluscan Studies*, **78**: 92–99.

RAUT, K. & BARKER, G.M. 2002. Achatina fulica Bowdich and other Achatinidae as pests in tropical agriculture. In: *Mollusks as crop pests* (G.M. Barker, ed.), pp. 55–114. CABI Publishing, New York, NY, USA.

RICHARDSON, A. 1975. Food, feeding rates and assimilation in the land snail *Cepaea nemoralis* L. *Oecologia*, **19**: 59–70.

SCHAMP, B., HORSÁK, M. & HÁJEK, M. 2010. Deterministic assembly of land snail communities according to species size and diet. *Journal of Animal Ecology*, **79**: 803–810.

SMYTH, G. 2006. Statmod: Statistical Modeling. Compare groups of growth curves. R package version 1.2.4.

SPEISER, B. & ROWELL-RAHIER, M. 1991. Effects of food availability, nutritional value, and alkaloids on food choice in the generalist herbivore *Arianta arbustorum* (Gastropoda: Helicidae). *Oikos*, **62**: 306–318.

U.S. DEPARTMENT OF AGRICULTURE, A.R.S. 2012. USDA National Nutrient Database for Standard Reference, Release 25. Online at: http://ndb.nal.usda.gov/ (last accessed 9 February 2013).

WACKER, A. & BAUR, B. 2004. Effects of protein and calcium concentrations of artificial diets on the growth and survival of the land snail *Arianta arbustorum*. *Invertebrate Reproduction & Development*, **46**: 47–53.

WEBB, G.R. 1942. *Mesodon appressus* (Say) in Marion County, Indiana. *Nautilus*, **56**: 61–62.

WILLIAMSON, P. & CAMERON, R. 1976. Natural diet of the landsnail *Cepaea nemoralis*. *Oikos*, **27**: 493–500.

ZAR, J.H. 1996. *Biostatistical analysis*. Edn 3. Prentice-Hall, Upper Saddle River, NJ.