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Life history strategy of *Bradybaena similaris* (Fèrussac, 1821) (Mollusca, Pulmonata, Bradybaenidae)

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Abstract

Bradybaena similaris (Férussac, 1821), commonly known as the Asian trampsnail, is a land snail originally native to Asia and introduced in other regions of the world through commerce in plants and produce. In Brazil, populations of this species are well established and distributed from the state of Amapá in the north to Rio Grande do Sul in the south. This land snail is easily raised in the laboratory and has been used as a biological model in studies of patterns of growth and reproduction, as well as behavioral, physiological and biochemical strategies related to starvation. In the present work, the life history strategy of *B. similaris* was characterized. We determined the growth, reproduction and longevity patterns of this species, and the interrelationships of these traits. Our results show that the life history of *B. similaris* is characterized by a combination of short life, short juvenile lifespan, early sexual maturity and few reproductive events, with a high reproductive effort in each event and high mortality shortly after the first reproduction. We conclude that there is a relationship between growth, reproduction and longevity patterns of *B. similaris*. This relationship is due to a differential allocation of energy between somatic growth, homeostasis and reproductive activity; which determines a life history pattern that tends to *r*-strategy.

Key words: Growth; longevity; reproduction; r-strategist species.

Introduction

The elucidation of life strategies can be useful in studies of ecology, evolution and phylogeny, behaviour, and reproductive biology. Moreover, this knowledge is essential to delineate management strategies for land snail populations at risk of extinction, control of pest populations (Picoral and Thomé 1989), as well as control of parasite populations that use molluscs as intermediate hosts (D'ávila *et al*. 2004). Life history strategies of terrestrial molluscs may be resolved when the relationships between growth, reproduction and longevity patterns are clarified.

The majority of the studies on the longevity of terrestrial molluscs and its relationship with life history traits involve species from temperate regions (Baur and Baur 2000; Heller 2001; Hommay *et al.* 2001; Ocaña 2003). Few studies of the life strategy of these animals have been conducted in tropical regions such as Brazil.

Bradybaena similaris (Férussac, 1821) is a land snail native to Asia, but has been introduced in other regions of the world through trade in plants and plant produce (Junqueira and Bessa 2004). In Brazil, populations of this species are well established and distributed from Amapá to Rio Grande do Sul (Almeida and Bessa 2001). *B. similaris* is easily raised in the laboratory and has been used as a biological model in studies seeking to clarify growth and reproduction patterns, as well as behavioral, physiological and biochemical strategies related to starvation (Pinheiro 1996; Lira *et al*. 2000; Moreira *et al*. 2003). However, none of these studies have specifically addressed the life strategy of *B. similaris*.

In the present work the life history strategy of *B. similaris* was characterized. We determined the growth, reproduction and longevity patterns of this species, and the interrelationships of these traits.

Methods

Raising of the snails

Laboratory colonies were established on newly hatched specimens collected in the municipality of Juiz de Fora, Minas Gerais and kept in transparent plastic dishes (14cm in diameter, 9cm in height), with 30 individuals per dish in three replicates. The experimental groups underwent the same treatment. The bottom of each dish was lined with humus, which was moistened every two days with 10 ml of water. The snails were fed *ad libitum* with a commercial poultry feed (comprising a mixture of corn meal, soy meal, wheat bran, gluten bran, cornmeal, chicken flesh and bone meal, fish meal, calcium phosphate, sodium chloride) supplemented with a premix of minerals, vitamins and calcium carbonate. The snails were kept at room temperature and under natural light conditions. This study was carried out from September 2004 to January 2006, for a total of 488 days. All the procedures employed in the present study were approved by the ethics committee in animal research of Juiz de Fora Federal University (protocol number 49/2003-CEA).

Observations on growth, reproduction and survival

To characterise life history traits of *B. similaris*, we quantified for each replicate colony the pattern of survival,

changes in mean animal size, the date of onset of oviposition activity and the daily reproductive output.

The size of each snail was determined by measurement of shell diameter using a Kanon caliper to 0.1 mm precision. Up to the age of 90 days shell diameters were measured at 15-day intervals. Thereafter, measurements were undertaken at 30-day intervals.

The first presence of eggs in the terrarium was taken to indicate that the snails had reached sexual maturity. To record deaths, the number of oviposition events, and the numbers and sizes of eggs clutches, the snails were observed daily from the first presence of eggs until death of the last individual. Growth rate was calculated as the differences in changes in shell diameter divided by number of days between the measurements.

The data were expressed as means per replicate and then averaged across the three replicates to provide parameters of life history traits applicable to groups of 30 snails. These data were subjected to variance analysis (ANOVA) to detect differences in growth of the snails during the juvenile (before the first oviposition event) and adult phases of the life cycle.

Results

Growth

There was no statistical difference in changes of mean shell diameter between the three replicate groups of snails (p=0.6554).

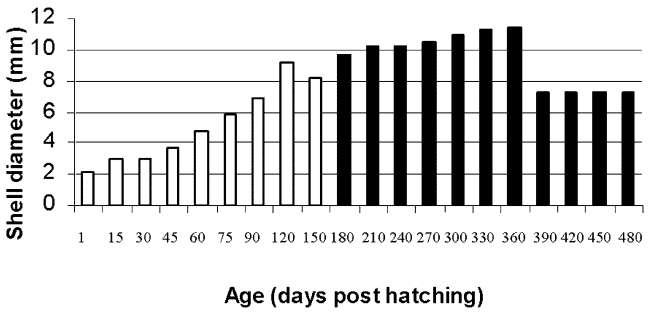

FIGURE 1. Temporal trend in shell diameter averaged across individuals in colonies of *Bradybaena similaris* established from 30 hatchling snails. Note: Data are shown for individuals surviving at measurement dates (see Table 1). White columns represent juvenile stage and black columns represent adult stage.

The growth of the snails was monitored for 480 days post-hatching (64 weeks) (Table I). Nevertheless, the longevity of the longest surviving individual was 488 days (65 weeks). The mean shell diameter continued to increase after the first oviposition, which occurred between Day 160 and Day 193, with a mean 172.3 days per replicate (Fig. 1), indicating variation among individuals in age to onset of reproductive activity. However, these data on mean shell diameter are potentially confounded by the death of reproductively-spent individuals. Nonetheless, growth rate in shell diameter was less pronounced (p=0.0327) during the adult stage (0.25 mm/day) than in the juvenile stage (0.43 mm/day). The greatest rate of shell growth, 0.08 mm/day, occurred between Days 90 and 120 in the juvenile stage. From about Day 390, in the adult stage, mean shell diameter was relatively stable, indicating cessation of shell growth in most surviving individuals. The rate of shell growth during the adult stage was negative for some measurement intervals, indicating death of larger individuals. The greatest mean diameter, 11.4 mm, was recorded at Day 360. The greatest absolute diameter, 14.0 mm, was recorded for an individual at Day 150 (Table 1).

TABLE 1. Temporal trend in mean size of individuals (as indicated by measurement of shell diameter) in colonies of *Bradybaena similaris* established from 30 hatchling snails.

Days post-hatching	Mean number of snails alive	Growth rate during interval (mm/day)	Shell diameter (mm)			
			Mean	s.e.	Min.	Max.
1	30	-	2.1	0.2	1.5	3.0
15	18	0.060	3.0	0.4	2.2	4.3
30	18	0.000	3.0	0.6	1.7	5.0
45	16	0.050	3.7	0.7	1.9	6.8
60	16	0.070	4.7	0.8	3.1	7.6
75	16	0.070	5.8	1.3	3.0	8.8
90	15	0.070	6.9	1.9	3.7	10.6
120	15	0.080	9.2	2.4	4.2	11.9
150	15	- 0.030	8.2	2.0	4.5	14.0
180	10	0.050	9.6	1.7	4.2	12.7
210	7	0.020	10.2	1.5	4.5	12.7
240	6	0.000	10.2	1.1	4.8	12.7
270	5	0.010	10.5	0.8	9.5	13.0
300	4	0.010	10.9	0.7	9.5	13.0
330	3	0.010	11.3	0.3	9.7	13.0
360	3	0.003	11.4	0.2	9.8	13.0
390	3	- 0.140	7.2	0.2	9.8	12.2
420	3	0.000	7.2	0.1	9.6	12.3
450	2	0.003	7.3	0.2	9.9	12.4
480	2	0.000	7.3	0.2	9.9	12.4

Reproduction

The reproductive period occurs between Day 160 and Day 436 (Fig. 2). Each group of snails produced on average 22 egg clutches and a total of 2700 eggs over the lifespan of the colony. The number of eggs per clutch ranged from 1 to 202. Thus mean daily reproductive output during the adult stage varied between 0 and 398 eggs, or 0 to 79.5 eggs per individual present. For each of the juvenile snails used to establish the colonies, the subsequent life-long output averaged 30 eggs. The mean number of eggs per clutch varied between 3.0 and 115.5.

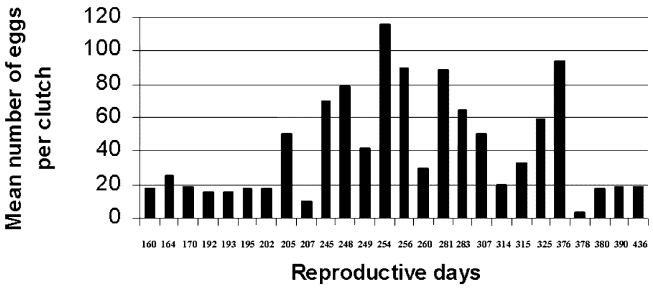

FIGURE 2. Mean number of eggs per clutch of *Bradybaena similaris* over the entire reproductive period.

Mortality

The mean longevity for individuals was 144.36 days (range 15–488 days). Pronounced mortality across replicates was observed at the juvenile stage, with only 39% of the individuals reaching reproductive maturity (Fig. 3). Most of this mortality occurred in the first 15 days (2 weeks). There was also a distinct pulse of mortality during the period of transition from juvenile to adult stages and the onset of oviposition activity. Thereafter, the mortality rate among snails classed as adults was more or less constant (Fig. 3).

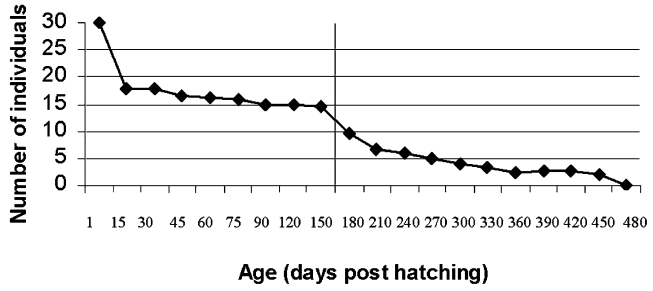

FIGURE 3. Temporal trend in survivorship in colonies of *Bradybaena similaris* established from 30 hatchling snails. Vertical line indicates onset of oviposition activity.

Discussion

Studies of the life history strategies of land snails are fundamental to elucidate how these organisms allocate energy resources over the course of their lives to enhance fitness (Cichón 1999; Norton and Bronson 2005). The patterns of resource allocation to reproduction and growth in land snails are associated with different life history strategies, selected in the course of evolution (Antkowiak and Chase 2003).

There are two kinds of resource allocations during a lifespan. In the most common pattern, after birth all energy excess to maintenance of bodily functions is directed to growth until the individual attains sexual maturity. After maturity, growth may be interrupted and energy is directed to reproduction. This pattern characterizes determinate growth. The second pattern, that of indeterminate growth, is characterized by continued growth after maturity and terminated only by death (Cichón 1999).

The results of the present study indicate that *B. similaris* continues to grow after sexual maturity. However, the growth during the adult stage was much less pronounced than in the juvenile stage, implying that energy resources are mainly allocated to the reproductive effort. These findings were confirmed by the high mortality that occured shortly after sexual maturity, probably due to depletion of energy reserves needed to maintain homeostasis. Due to the variable age at which individuals attained sexual maturity, this apparent continued growth after onset of oviposition activity in the colonies can be attributed to some late-maturing individuals still being in a phase of shell growth. Thus *B. similaris* can be interpreted as having determinate growth.

Several studies of the biology and reproductive behavior of land snails address how the life history patterns are associated with energy allocation (Raut and Panigrahi 1988; Reise 1995; Ocaña and Emson 1999; Parmakelis and Mylonas 2002; Antkowiak and Chase 2003; Ilano *et al*. 2004; Haase and Karlsson 2004; Evanno *et al*. 2005). The resources available for different biological processes are limited. Thus, tradeoffs must exist between life history traits such as reproduction, growth and longevity. For example, delaying reproduction by increasing the time to reach sexual maturity can lead to increased longevity (Zera and Harshman 2001), a short lifespan may be associated with maximum reproductive effort in a few events (Baur and Baur 2000), and the mortality rate may increase with aging, being highest just after reaching sexual maturity (Staikou *et al*. 1990).

Terrestrial gastropods were classified by Heller (2001) into two categories: semelparity—short-lived species, which live for at most two years and reproduce in only one season, and iteroparity—the long-lived species, which live for more than two years and reproduce in at least two seasons. However, the information reviewed by Heller mostly concerned snails of temperate regions. Further, there was no clear resolution about the life history contexts that could favour strategies with a short lifespan over those with a long lifespan, especially for tropical species.

Another classification concerning life history strategies is *r* and *K*-selection (Krebs 1994). According to this classification, *r*-strategist species exhibit high reproductive effort over a short span and few reproductive events, with the combination of early maturity, numerous offspring, small juvenile size and short lifespan. *K*-strategist species show the opposite tendencies, with low reproductive output maintained over a long life and many reproductive events.

The results of the present study show that the life history of *B. similaris* is characterized by a combination of short life, short juvenile lifespan, early sexual maturity and few reproductive events over life, with a high reproductive effort in each event and high mortality shortly after the first reproduction. We might conclude from these traits that *B. similaris* is an *r*-strategist species. Short lifetime associated with great reproductive effort in few reproductive events was also observed for *Bradybaena fruticum* (Müller 1774) (Staikou *et al*. 1990).

Although the methodology employed in the present work (rearing under only one set of environmental

conditions) did not address the plasticity of life history traits, which is an important component of life strategy, the patterns of association between life history traits reflect the life strategy. The phenotypic plasticity in life history traits, in response to environmental conditions, is not enough to change the general pattern of association between life history traits such as longevity, growth and reproduction. The features of life strategies are determined by intrinsic factors, which are genetically determined and reflect the evolutionary history of species. Changes in life history traits determining shifts in life history strategy, as an adaptive response, can only occur over evolutionary time. Many authors state that *r*-selection may occur in variable environments, where the survivorship of adults is unpredictable. Thus, in such a context, natural selection will favour a short lifespan and a maximal, opportunistic reproductive effort during transient favorable periods. Several studies have demonstrated that *B. similaris* is physiologically adapted to survival over transitory unfavorable environmental conditions (Pinheiro 1996; Lira *et al*. 2000; Moreira *et al*. 2003), supporting the idea that the species evolved in environments where conditions favorable to survivorship and reproduction are inconsistent, leading to *r*-selection.

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