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THE EFFECT OF PARENT BODY SIZE ON THE EGG SIZE AND OFFSPRING GROWTH IN *HELIX POMATIA* LINNAEUS, 1758 (GASTROPODA: PULMONATA: HELICIDAE)

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ABSTRACT: The experiment on adult Roman snails (*Helix pomatia* L.) and their offspring showed a positive correlation between the mean egg size and the parent body size. There was no correlation between the parent size and the number of eggs. A trade-off between the egg size and the clutch size was observed. The body size of juveniles at early growth stages was correlated with the parent size; later (offspring aged 2 and 3 months) there was no such correlation, suggesting maternal effect. The results are relevant to estimating the reproductive success and offspring survival rate at early stages.

KEY WORDS: *Helix pomatia*, Roman snail, body size, maternal effect, shell size, offspring quality

INTRODUCTION

The Roman snail's history has been associated with that of humans for centuries. Being synanthropic in much of its range, the species is naturally influenced by anthropogenic factors. Its biology (KILIAS 1960, URBAŃSKI 1963, DZIABASZEWSKI 1975), ecology, and economic importance have been extensively studied (CADART 1955, TURČEK 1970, ŁOMNICKI 1971, POLLARD 1975, STĘPCZAK 1976, CHMIELEWSKI 2005, LIGASZEWSKI et al. 2007). *H. pomatia* shows a wide range of shell size variation (URBAŃSKI 1963, STĘPCZAK 1982, DYDUCH-FALNIOWSKA et al. 2001, ANDREEV 2006); the growth rate varies individually even among snails from the same clutch (POLLARD 1975). Since the body size is an important life history trait (ROFF 1992, STEARNS 1992), the explanation of this variation would be important from the scientific and practical point of view.

It is possible to assess individual condition and habitat quality based on the Roman snail body size (STĘPCZAK 1982, DYDUCH-FALNIOWSKA et al. 2001, ANDREEV 2006). It is also possible to estimate the individual age, and even conditions in particular years, based on winter growth bands on the shell (RABOUD 1986, NEVES & MOYER 1988). The body size of Roman snail is important for economic reasons; in natural populations individuals with shell diameter exceeding 30 mm have been quite heavily exploited for many years (HEIN 1952, STĘPCZAK 1976, ŁYSAK 1999, ROZPORZĄDZENIE MINISTRA 2004). The mechanisms responsible for the phenotypic variation in *H. pomatia* are mostly unknown, and the information on the growth rate and size is insufficient (LIGASZEWSKI et al. 2005). On the other hand, the knowledge about factors controlling the snail's growth and body size is crucial for future protection strategies.

The aim of this study was to answer the following questions: 1. Does parent body size affect the offspring quality?; 2. Is there a relationship between the number of eggs produced and their quality?; 3. Is there a correlation between the parent and offspring body size?

MATERIAL AND METHODS

Adult Roman snails were collected from a wild population in Balice (50°05'39"N, 19°48'43"E) at the beginning of May 2005 and moved to the field culture in the National Research Institute of Animal Production in Balice (experimental heliculture centre). Their sexual partners were not known. In the first decade of June 2005, 45 parent snails with their first clutches of the season were obtained from the culture. The snails were weighed and measured (shell width, height, and diameter, according to STĘPCZAK 1982) and then released. The incubation started on June 6th 2005, the experiment was concluded in the 3rd decade of November 2005. Eggs in every clutch were counted, weighed and their diameter was measured to the nearest 0.1 mm. The total number of eggs in all samples was 2,098. On the 8th of June 2005 all the egg clutches were placed in plastic cuvettes, at ca. 25°C, substratum humidity of ca. 90% and natural daylight. Initially, the juveniles were kept in small cuvettes in which they hatched. Big clutches were divided between several cuvettes to avoid overdensity. The offspring feeding started when most juveniles had left the nest and moved to the cuvette cover. The feed used for farm snail cultures was used, at first enriched with a mixture of chalk and soil. Young snails were fed ad libitum.

In order to monitor individual growth, the juveniles, when aged approximately 3 weeks and with ca. 6 mm shell width, were individually marked with transparent plastic labels (4.5 × 3 mm). All the labels bore waterproof printed 4-digit codes; the first two digits represented the parent number, the last two digits – the offspring number (Fig. 1). Next, young snails were moved to common garden culture, with a density of ca. 400 individuals/m^2 (2–6 July 2008), (SOWIŃSKI & WĄSOWSKI 2000, ŁYSAK et al. 2001). The boxes were filled with a soil layer several centimetres thick; the soil was prepared so that its structure/granulation, pH and moisture resembled such parameters of the usual substratum in the natural Roman snail habitats. The humidity in the boxes was 70–90%, the lighting regime was natural and the temperature varied according to external conditions. The maintenance followed LIGASZEWSKI's instructions (LIGASZEWSKI, personal communication, ŁYSAK et al. 2001). The size measurements (STĘPCZAK 1982) were taken three times: on July 7th, August 11th and September 11th, 2005. When the experiment was concluded, the marked snails were released into their natural habitat; the marking stayed on their shells for at least three years.

Fig. 1. Individually marked Roman snail

The size of eggs and juveniles versus parent shell size were subject to regression analysis. Since the shell width, height, diameter and body mass are highly correlated (STĘPCZAK 1982), Principal Component Analysis (PCA) was applied in order to reduce the number of variables (MANLY 1986). PCA showed that the first component (PC1) for the set of parent shell dimensions best summarized the overall data variation (Table 1) and was thus chosen for further analysis. Similarly, the first principal components for the shell size of juveniles aged 3 and 6 weeks were used for statistical analyses because they best explained the total variation.

Table 1. Principal components analysis for shell size of parent-snails and offspring aged 3, 8 and 12 weeks. Eigenvectors are given for PC1

	Parent	3rd week offspring	8th week offspring	12th week offspring
Percent of described variation				
PC1	76.88	95.26	97.55	97.84
PC2	10.95	3.58	2.03	1.92
PC3	7.90	1.16	0.42	0.25
PC4	4.29			
Eigenvectors of shell size				
height	0.48	0.58	0.58	0.58
width	0.50	0.57	0.58	0.58
diameter	0.52	0.58	0.57	0.57
weight	0.51	–	–	–

RESULTS AND DISCUSSION

The total of 928 juveniles hatched from the 2,098 eggs. The mean percentage of surviving eggs per clutch was 48% (SD±2.7). The mean survival of juveniles on the 1st control date was 51% (SD±24.8), on the 2nd date – 47% (SD±24.4), and on the 3rd date – 46% (SD±24.5). The mean egg diameter was 5.17 mm (Table 2). The mean shell height, width and diameter for juveniles aged 3 days were 6.38, 7.70 and 4.51 mm, respectively (Table 2). The mean egg diameter was negatively correlated with the clutch size (R=–0.56, N=45, P<0.001). This confirmed the classical trade-off in energy allocation between the offspring quality and quantity (PARKER & BEGON 1986).

Larger snails laid bigger eggs which in turn produced larger juveniles (Table 3 and 4). This may result from heritability of body size or from maternal effect, where the offspring body size is a function of the parent's condition and reflects habitat quality (BERNARDO 1996). There was no correlation between the clutch size and the size of juveniles aged 8 and 12 weeks (R=0.06, N=37, P=0.716 and R=0.007, N=37, P=0.969, respectively). Similarly, we observed no significant correlation between the parent body size and the clutch size (Table 3). There was a positive correlation between the parent and offspring body size only in the first weeks of offspring life. The shell size of older juveniles was not correlated (or the relation was weak) with the parent size (Table 3). Similarly, the correlation between the clutch size and the offspring shell size was only significant for the youngest offspring (Table 4). This may be due to maternal effect which could act on the egg size, and then become gradually less pronounced.

Shell size differences between wild populations of Roman snail are often significant (STĘPCZAK 1982). Considering the short distances covered by the snails (DENNY 1980), it can be assumed that migrations between populations are negligible. Individuals living in different habitats may differ in morphology. Such morphological differences have been recently found by DYDUCH-FALNIOWSKA et al. (2001). It is not known if they are genetic, a result of phenotypic plasticity with great reaction norms, or an effect of genotype-environment interactions (FALCONER & MACKAY 1996, LYNCH & WALSH 1998). The Roman snail lays eggs several times during one season (STĘPCZAK et al. 1982, STĘPCZAK 1992); eggs laid by breeding snails in the spring, summer and autumn differ in quality and quantity (LIGASZEWSKI et al. 2007). The date of egg-lying may thus influence the size and number of eggs. Extending our studies to all egg clutches produced during the whole season or even life time could provide valuable information on the reproductive strategy of the Roman snail.

Table 3. Matrix of correlation between first principal component of parental body size (PC1 of parent) and mean eggs mass, number of eggs, first principal component of shell size of offspring aged 3 weeks (PC1 of 3rd), first principal component of shell size of offspring aged 8 weeks (PC1 of 8th) and first principal component of shell size of offspring aged 12 weeks (PC1 of 12th). * – correlation significant at 0.05; ** – correlation significant at 0.01

PC1 of parent	Mean egg mass	Eggs number	PC1 of 3rd	PC1 of 8th	PC1 of 12th
R	0.35*	–0.07	0.48**	0.16	0.10
N	45	45	37	37	37
P	0.017	0.628	0.003	0.329	0.538

Table 2. Measurements of: eggs and juveniles aged 3 days. N – number of analysed clutches; Mean – mean number per clutch; SD – standard deviation; Min – Max – minimal and maximal value in all samples of clutches; CV – coefficient of variation

Parameter	N	Mean	SD	Min–Max	CV
N clutch	45	45.7	15.68	3–83	0.34
Mean egg diameter in a clutch	45	5.17	0.38	4.1–6.1 [mm]	0.07
Mean offspring shell height in a clutch	37	6.38	0.76	5.4–9.3 [mm]	0.12
Mean offspring shell width in a clutch	37	7.7	0.77	6–10.5 [mm]	0.09
Mean offspring shell diameter in a clutch	37	4.51	1.64	3.6–13.9 [mm]	0.36

Table 4. Results of multiple regression analyses for two models: 1 – influence of batch mass and number of eggs on mean egg diameter; 2 – influence of mean egg diameter and number of eggs on PC1 of shell size in offspring aged 3 weeks

Model	Response variable	Factors	Estimate	SE	t	p
1	Mean egg diameter	Batch mass	0.209	0.024	8.80	<0.0001
		Eggs number	–0.027	0.003	–9.36	<0.0001
2	PC1 of 3-week offspring size	Egg diameter	3.015	0.980	3.07	0.004
		Eggs number	–0.017	0.021	–0.83	0.411

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