MAJOR FITNESS COMPONENTS IN LIFE HISTORY OF EURYOECIOUS LAND SNAIL *TROCHULUS HISPIDUS* (LINNAEUS, 1758) (GASTROPODA: HYGROMIIDAE)

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ABSTRACT: The life history of *Trochulus hispidus* (L.) over two generations was studied under laboratory conditions. In this semelparous, short-lived species, in which the juvenile lifespan constitutes almost three quarters of the whole life, substantial juvenile mortality is accompanied by a very high reproductive rate. The snails become reproductively mature at the age of one to two years; the growth rate varies greatly even among hatchlings from the same brood; the size of such siblings may differ by as much as two whorls at a single moment of time. These differences result in a spread of the reproductive period within a population over the whole active season. We hypothesize that this may spread risks where mortality is high and may be concentrated in short periods of adverse conditions. While full-sib matings among the offspring generation result in a 60% reduction in the proportion of ovipositing pairs relative to the parental generation, in those that do lay there are no differences in batch size or juvenile survival. It seems possible that avoidance of any inbreeding depression depends on pre-zygotic selection.

KEY WORDS: bet-hedging strategy, life history variation, differential growth rates, breeding success, inbreeding depression, hermaphrodite, laboratory conditions

INTRODUCTION

The principal aim of life history theory, a branch of evolutionary ecology, is to explain the remarkable diversity in life histories among species (FABIAN & FLATT 2012). Age at first reproduction, reproductive lifespan, and the number and quality of offspring are among the major life history characteristics. These traits vary with the nature of the threats and opportunities faced; the study of trade-offs between them lies at the core of life history theory (STEARNS 1989) and provides an explanation for the widespread variation of life history traits in natural populations (REZNICK 1985, ROFF 1992, STEARNS 1992). Of particular interest in this context are euryoecious species that may spread and occupy places differing greatly in environmental conditions both spatially and from season to season in the same place. Plasticity in life history is to be expected in such species.

The European hermaphroditic land snail *Trochulus hispidus* (Linnaeus, 1758) of the family Hygromiidae is such a euryoecious species. It has a broad geographic and altitudinal range, and inhabits a wide variety of habitats: from anthropogenic to rocky alpine sites (PRÓĆKÓW 2009, DUDA et al. 2011). Earlier attempts to establish its life history parameters in the laboratory have been frustrated by very heavy juvenile mortality of *Trochulus* (CAIN 1959, FALKNER 1973, PRÓĆKÓW et al. 2013), and this is probably the reason for the fragmentary data scattered in the literature (JEFFREYS 1862, TAYLOR 1916, FRÖMMING 1954, CAMERON 1982).

Recent combined laboratory and field observations from S.W. Poland, however, have established some life cycle parameters in *T. hispidus* (PROĆKÓW et al. 2013). While it is a nominally semelparous species, the reproductive period is relatively long (extending up to seven months in the field but in laboratory conditions so far studied limited to spring and summer) and several batches may be laid. The potential reproductive capacity is great as it produces a large number of eggs and a high proportion of hatchlings (PROĆKÓW et al. 2013). However, it is affected by a high juvenile mortality which is known also in the case of other hygromiids (CHATFIELD 1968).

Our study was focussed on the life history of *T. hispidus* based on four-year laboratory observations for two generations. Furthermore, we wanted to assess how much of the inter-individual variance in lifetime fecundity, fertility and survival could be attributed to different traits such as reproductive lifespan, age at first reproduction and growth rate.

MATERIAL AND METHODS

The laboratory culture was established on May 2012 and lasted till March 2016. The material (20 juveniles) originated from two sites in Lower Silesia, S.W. Poland: Lubawka (50°42'19.2"N, 16°00'09.8"E, 420 m a.s.l.) and Wrocław (51°07'16.9"N, 16°50'38.7"E, 130 m a.s.l.). Ten pairs, each consisting of two snails from the same population, were kept in plastic containers of 12×7×5 cm, with bottoms covered with tissue paper and moist soil to encourage egg-laying. Additionally, litter from the habitat was used as substratum. Dolomite tablets served as a supplementary source of calcium. Snails were maintained in a climate chamber on a light/dark 12/12 photoperiod at 22°C and 15°C, respectively, and 80% relative humidity. Food (e.g. lettuce, carrot) was provided as needed.

Eggs and newly hatched snails were removed to Petri dishes to prevent double counting on subsequent occasions. Each batch (brood) was then kept separately. Twenty four pairs of snails from the offspring generation were established, in which both members of each pair came from the same brood. As with the parental generation, each brood was removed once it had appeared. The following life history traits were recorded for snails coming from the two (parent and offspring) generations: batch size, number of eggs per pair (fecundity), hatching success (fertility) and juvenile survival. We also recorded the age at first oviposition (juvenile lifespan), as well as reproductive, post-reproductive and adult lifespan for single pairs. The only parameter calculated per individual was the whole life span of the offspring generation snails. Additionally, it was possible to measure the growth rate (EHRMANN's 1933 method of counting whorls) within and between 19 randomly selected broods in the offspring generation (n = 109 snails). To collect data about growth rates at different densities snails were kept in groups of 2–5 (n = 13) and 6–15 individuals (n = 6). Because the differences in all traits of both populations were not significant the results were pooled.

We defined the reproductive lifespan as the time elapsed between production of the first and last egg, the post-reproductive lifespan as the period between last reproduction and death and the adult lifespan as the period from first reproduction to death. All these parameters refer to the parent generation except the juvenile lifetime which was derived from the offspring generation. Mann-Whitney U-test was used to compare traits of snails in the two generations. Spearman correlations were calculated between the different life history traits.

RESULTS

The reproductive capacity (proportion of ovipositing pairs) of the ten parent pairs originating from the field was 100%, whereas in the offspring generation only nine pairs (37.5%) laid eggs. Those hatching in spring and summer were significantly more likely to lay than those hatched in autumn (7 out

Table 1. Lifetime fecundity, fertility and survivorship of *T. hispidus* kept over two generations. Means ± SD and ranges in parentheses, p-values resulting from Mann-Whitney U-tests are not significant (n.s.). [a] data denote to F_1 offspring generation, [b] data denote to F_2 offspring generation

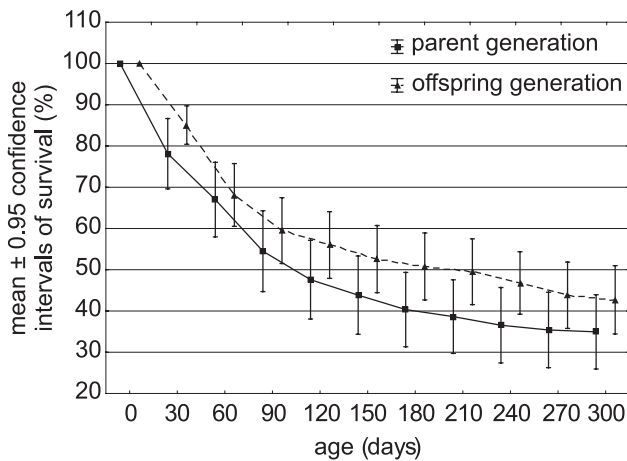|	Parent generation	n	Offspring generation	n	p
Batch size	15.5 ± 11.2 (3–47)	36	25.4 ± 14.6 (6–53)	30	n.s.
No. eggs/pair	68.1 ± 51.4 (8–164)	10	61.6 ± 44.4 (24–124)	9	n.s.
Hatching success (%)	84.6 ± 21.7 (22–100)	37	65.7 ± 16.8 (41–100)	31	n.s.
Survival until age of 300 days (%)	25.3 ± 27.8 (0–100)[a]	39	29.5 ± 24.1 (0–100)[b]	36	n.s.

Fig. 1. Temporal trends in survivorship of *T. hispidus* hatchlings derived from parent (squares) and offspring (triangles) generations

Fig. 3. Variation in shell size (measured as number of whorls) at different ages in *T. hispidus* at a single moment of time

of 11 pairs in spring and summer; 2 out of 13 pairs in autumn, $\chi^2 = 5.9$, $p < 0.05$). While those laying in autumn were slightly older than those laying in spring and summer, the difference was not significant. The age at first oviposition for a pair ranged between 382 and 759 days, roughly between one and two years old.

Life history traits were highly variable within the generations. The differences in lifetime fecundity, fertility and survival of *T. hispidus* among the generations were not significant (Table 1).

The snails of both generations produced similar numbers of eggs (Table 1). The parent pairs laid between 8 and 164 eggs (mean 68.1) and thus showed a 20-fold intra-group variation in lifetime fecundity. The offspring pairs laid between 24 and 124 eggs (up to 5-fold variation). The mean batch size increased in the offspring generation and SD was also higher than in the parent generation. The snails of both groups showed no statistically significant differences in their hatching success or survivorship until the age of 300 days after hatching and they had similar SD values (Table 1). The survivorship in relation to age in the two generations is shown in Fig. 1.

The reproductive lifespan (for a pair) in the parent generation varied between 1 and 328 days (mean 103 days, SD = 98, n = 10). The mean post-repro-
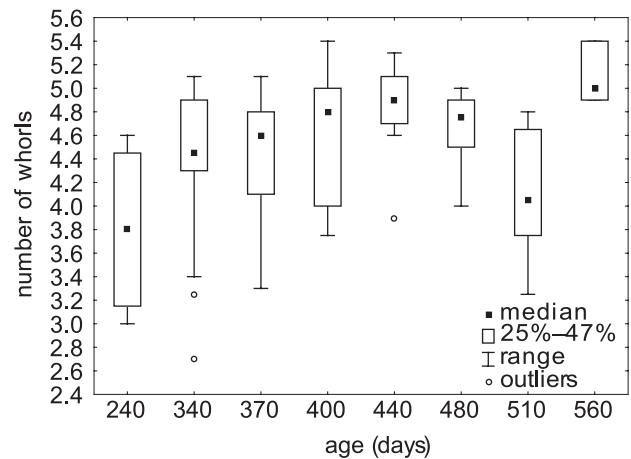
ductive lifespan was 102 days (range 11–336, SD = 101), hence the adult lifespan of approximately 205 days (range 30–382, SD = 121). The proportions of mean juvenile, reproductive, post-reproductive and adult lifespan for a single pair are shown in Fig. 2, which is a composite, using information from both generations.

The growth of snails in 19 broods was monitored for between 240 and 560 days post-hatching (Fig. 3). The growth rate expressed as the whorl increment varied widely; the snails of the same age were various sizes. The widest ranges and thus the largest differences were recorded for the youngest snails (Fig. 3). Similar results were obtained when comparing the growth within broods, where the SD values of the whorl numbers ranged from 0.1 to 0.75. A comparison of the growth rate in broods with low (2–5 snails) and high (6–15 snails) densities revealed no statistically significant differences (p > 0.05).

None of the correlations among life history variables for the parent generation, including the survival and growth of the offspring, achieved statistical significance, but there were some suggestive negative associations such as those between the number of eggs per pair and subsequent hatching success and survival.
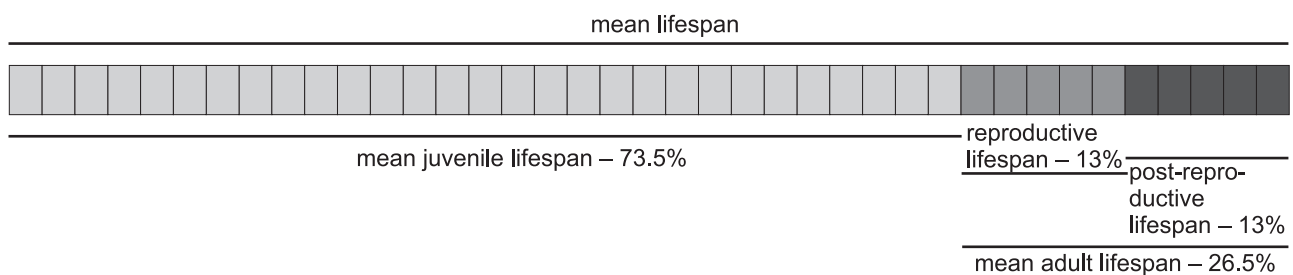

Fig. 2. Proportions of mean juvenile, reproductive, post-reproductive and adult lifespans derived from two generations for single pairs of *T. hispidus*

DISCUSSION

The trade-offs in any reproductive strategy should, in principle, optimise traits for reproductive success (STEARNS & HOEKSTRA 2005). Where the environment may alter over short distances and even from one season to the next, a bet-hedging strategy may represent an optimum, especially for animals like land snails with limited dispersal capacity. Although snails display a variety of life history strategies (e.g. LOCHER & BAUR 2002, ANTKOWIAK & CHASE 2003, HAASE & KARLSSON 2004, EVANNO et al. 2005, BEEBY & RICHMOND 2007), many have an essentially semelparous pattern of reproduction and a relatively short life span. Typically, such species have high reproductive rates and high losses at the egg or juvenile stages (BAKER 1991).

T. hispidus fits into this common pattern (PROĆKÓW et al. 2013). It has a short life span, a high reproductive output, and it is semelparous in the sense that although it may lay more than one batch, adults do not survive to breed in more than one season. There are further features of its reproductive strategy that seem particularly suited to a locally unpredictable environment and also to a very wide range of habitat conditions across its distribution range (PROĆKÓW 2009, DUDA et al. 2011). High but variable mortality unconnected to relatively stable resources such as food but perhaps associated with fluctuating water and temperature regimes may account for its short-lived, fast-reproducing strategy. Certainly, *T. hispidus* was able not only to survive in the harsh climate of the glacial steppe (LOŽEK 1964), where it was a typical species, but also this strategy could be a preadaptation for its recent life history.

T. hispidus takes at least one year to become sexually mature, and the adults have a mean reproductive lifespan of ca. 103 days, and a maximum of 328 days (estimated from single pairs). What is interesting and unexplained is the further period of post-reproductive life (mean 102 days, maximum 336 days). While it may be a product of laboratory conditions, this post-reproductive period suggests that the snails do not exhaust themselves completely having produced the last batch, as there may be later opportunities to lay if conditions are right. Similarly, the basically semelparous and unrelated *Vertigo pusilla* may survive for a longer time and reproduce again, which is also evident from histological studies on its post-reproductive gonad (MAZURKIEWICZ & POKRYSZKO 2005).

The extended period of reproductive life, often involving laying more than one batch, and the evidence that adults do not die immediately after their last reproduction indicate that, although formally semelparous, *T. hispidus* is far from the extreme form of this reproductive strategy where a single batch is followed by death. It allows for a flexible response to variable conditions within any one season.

There is more evidence of bet-hedging in this species. We recorded considerable variability in growth rates within broods. Juvenile activity, feeding and growth may be limited by a high concentration of mucus and other density-related factors (SANZ SAMPELAYO et al. 1990, COOK 2001, HANLEY et al. 2003). In other species, growth was constrained by density (DAN & BAILEY 1982, JESS & MARKS 1995), but our work did not show such an effect in *T. hispidus*. Differential growth rates were documented between populations and within broods of *Cornu aspersum* (BEEBY & RICHMOND 2007). Maternal adjustment of egg size produced enormous variation in growth and developmental rates in *Deroceras laeve*, even among siblings in identical conditions (SHIBATA & ROLLO 1988). While the functional significance of such variation is unknown, it at least suggests that reproductive strategy is finely tuned to changeable circumstances (SHIBATA & ROLLO 1988). Thus, to maximise fecundity in an environment with high and irregular levels of mortality, frequent production of offspring during a whole growing season can be a good strategy. This might be also promoted by producing different sized eggs or supplying additional nutrients (BEEBY & RICHMOND 2007). Some terrestrial gastropods produce infertile 'trophic' eggs that are consumed by early hatchlings, and in others early hatching juveniles may consume their developing siblings (BAUR 1992, DESBUQUOIS 1997). Our study did not examine the fate of eggs, but we did not observe any cannibalism.

This pattern of multiple batches, varying growth rates and a reproductive season spread over a considerable part of the year is known from field studies for a number of semelparous snail species, including *T. hispidus* (STAIKOU & LAZARIDOU-DIMITRIADOU 1990, PROĆKÓW et al. 2013, NYUMURA & ASAMI 2015).

The results in terms of reproductive output of the offspring generation need careful interpretation, as sib mating was involved. This may have influenced the readiness to mate and the production of viable eggs. In *Cornu aspersum* it was presumed that infertility in related snails arose from incompatibility or sterility (ALBUQUERQUE DE MATOS & SERRA 1984). It appears, however, that laboratory-reared snails copulate less readily than those taken from the field (CHEN 1993). As all our snails were raised entirely in constant laboratory conditions, laboratory effects may have prevented some individuals from copulating and reproducing. The observed reduction in reproductive capacity of *T. hispidus* might also come from inbreeding depression, i.e. mating between closely related individuals which as in *Arianta ar-*

bustorum can incur substantial fitness costs (CHEN 1993).

Thus, while there was a more than 60% reduction in the number of ovipositing pairs among the offspring relative to the parental generation, there were no differences in the output and juvenile survivorship among those pairs that did reproduce (Table 1). This reduction was much greater for pairs that had hatched in autumn than in those that hatched in spring and summer. As it takes at least one year before snails are able to lay their first eggs, the next generation will be ready to reproduce at the earliest approximately in the same season, while some will need longer. Growth rates and time to reach maturity are certainly affected by season. In the laboratory-reared land snail *Succinea putris* differences in the growth rate were dictated by the time of year (spring or autumn) rather than by the external conditions or the age of the juveniles (KUŹNIK-KOWALSKA et al. 2013). In *Cantareus apertus* the season of hatching had significant effects on the length of growth period and the weight of hatchlings. Spring snails took less time to develop and reached similar adult body weight as the autumn snails. Differences in the egg size or quality between the snails from different seasons were proposed as the explanations of this phenomenon (BENBELLIL-TAFOUGHALT & KOENE 2015). In some insects, it seems that cross-generational information can influence reproductive strategy (e.g. LEADBEATER & CHITTKA 2007, GIURFA 2012). What emerges from our study is that a nominally simple semelparous strategy is in fact a complex and flexible system that adjusts to very variable environmental conditions.

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