

Reproductive strategies and life histories in two distantly-related but ecologically similar hygromiid species kept under laboratory conditions

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The two land snail species *Trochulus striolatus* (C. Pfeiffer, 1828) and *Xerocampylaea erjavecii* (Brusina, 1870) are distantly-related within the Hygromiidae, and while geographically separated, have similar habitats. They are conchologically very similar in their shape. The growth, reproductive strategies and life histories of these species reared under constant laboratory conditions were studied in order to detect any similarities and differences between the species. In both species, isolated individuals did not reproduce; thus, uniparental reproduction appears not to occur. While morphological characteristics, such as the egg size and number of whorls at hatching and at sexual maturity, were relatively constant and similar in both species, there were differences in terms of the growth rate, age at first reproduction, output of eggs over the lifespan and in the pattern of mortality. While the range of variation within species was much greater in relation to these traits, it appears that *X. erjavecii* grows faster than *T. striolatus*: they become adults earlier; they have a shorter lifespan as adults, but less juvenile mortality; and individuals lay many more clutches, over a similar time span, laying more than five times as many eggs as *T. striolatus* over the course of the experiment. Under these admittedly artificial conditions, the individuals of both species (although more so in *X. erjavecii*) can lay more than one clutch over a period of more than two years, in an environment where no winter conditions were imposed. These results, which can also be compared with similar data for *Trochulus hispidus*, a species closely-related to *T. striolatus*, emphasise the fact that life histories, even among species of a similar size and habitat, may differ considerably. They also illustrate the difficulties inherent in laboratory studies of life histories.

Key words: fecundity, land snails, mortality, sexual maturity.

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The reproductive strategies and life history patterns among animals are a key part of their evolutionary response to the conditions in which they live (Stearns 1992). Lifespans, fertility, growth rates and the patterns of mortality all vary greatly, and can be related to the ecology of the species concerned. There are few complete studies of these that have

been conducted among terrestrial molluscs (Maltz 2003), because while some data can be obtained in the field, such as the changing patterns of shell sizes in cohorts over time and the adult mortality rate (Cameron 2016), information on the fertility and early mortality of species requires laboratory cultures that are somewhat removed from natural con-



ditions, which can be hard to interpret. It is known that these features vary greatly among land molluscs (Cameron 2016), and that there is a phylogenetic component involved, although members of the same family may differ (Nisbet 1974). At one extreme, there are slow-growing, iteroparous species; while at the other are semelparous species that grow quickly, and die soon after laying many eggs. The fertility rate (eggs per adult) and the size of the eggs do not always vary in parallel with these strategies, so there is no consistent r/K continuum in the life history dynamics (Stearns 1992).

In the very speciose land snail family Hygromiidae, recent work (Neiber *et al.* 2017) has revealed that *Trochulus striolatus* (C. Pfeiffer, 1828) and *Xerocampylaea erjavecii* (Brusina, 1870) belong to separate tribes Trochulini and Urticicolini within the subfamily Trochulinae, although earlier studies had placed them in the same genus, *Trochulus*, based on anatomical and conchological criteria (Kerney *et al.* 1983; Proćków 2009). The distributions of these species do not overlap: *T. striolatus* is a North-West-European species and *X. erjavecii* is a North-Western Balkan species (Proćków 2009). Nevertheless, the two species have shells that are remarkably similar in their shape and aperture (Fig. 1, and see Welter-Schultes 2012). They also appear to occupy a similar range of habitats, although precise data on

the ecological preferences of *X. erjavecii* is lacking (Welter-Schultes 2012; Duda *et al.* 2014; Proćków *et al.* 2017).

Knowledge about the reproduction and life histories in Trochulini, as delimited by Neiber *et al.* (2017), is extremely scarce. Complete life cycle data is known only in the case of one species, *Trochulus hispidus* (Linnaeus, 1758) (Proćków *et al.* 2013; Proćków & Kuźnik-Kowalska 2016). There is only fragmentary data scattered in the literature for a few other *Trochulus* species (Jeffreys 1862; Taylor 1916; Frömming 1954; Cain 1959; Falkner 1973; Cameron 1982). For Urticicolini, there is only information on the size of the hatchlings (1-1.3 mm) and egg-laying inside the soil in the case of *Urticicola umbrosus* (Pfeiffer, 1828) (Frömming 1954).

In the present study, we examined selected features of the reproductive biology and life history patterns in *T. striolatus* and *X. erjavecii*, in order to detect any species-specific differences between these distantly-related but ecologically and conchologically similar species. We relate these findings to earlier work on *T. hispidus*, as a close relative of *T. striolatus* (Proćków *et al.* 2013; Proćków & Kuźnik-Kowalska 2016).

Material and Methods

The source material (28 individuals of 4.1-5.0 whorls) of *T. striolatus* originated from Licques, France (50.7967°N, 1.9428°E, 81 m a.s.l.), while the material (17 individuals of 3.5-4.7 whorls) of *X. erjavecii* originated from Hrvatska Kostajnica, Croatia (45.2186°N, 16.5036°E, 126 m a.s.l.). In the laboratory, the initial population of *T. striolatus* laid 490 eggs, from which 185 young hatched. The initial population of *X. erjavecii* laid 371 eggs, from which 189 young hatched.

For both species, offspring between one and seven days old were arranged in groups of 10 individuals in 15 groups (150 in total for each species). Each group was kept in a plastic container measuring 15×12×7 cm, with the bottoms covered with tissue paper and moist soil to encourage egg-laying. The snails were maintained, constantly, in a climate chamber on a light/dark 12/12 photoperiod at 22°C and 15°C, respectively, and at 80% relative humidity. Food (e.g. iceberg lettuce and carrots) was provided as needed. Dolomite tablets were served as a supplementary source of calcium. In addition, the snails were sprayed with boiled, cooled water once a week. The boxes were inspected regularly and the mortality rate was recorded. A further 30 individu-



Fig. 1. Shells of (A) *Trochulus striolatus* from Licques, France and (B) *Xerocampylaea erjavecii* from Hrvatska Kostajnica, Croatia. Photos: Małgorzata Proćków.

als of each species were reared singly, in the same conditions, from an early juvenile stage in order to check for uniparental reproduction. The number of whorls on the survivors of the initial 180 hatchlings of each species (in groups and singly) were measured at 30-day intervals, following [Ehrmann \(1933\)](#).

There was some mortality in all the groups of both species over the course of the experiment, with the last survivor, a *T. striolatus*, living for 1589 days. Over the first 300 days, before any snail had become sexually mature, 70 out of 150 *T. striolatus* in the groups survived for the whole period (and 17 of the 30 reared singly). For *X. erjavecii*, the corresponding figures were 87 and 12. It follows that not all of the snails laid eggs, and the number capable of doing so declined as the experiment proceeded. As the snails reached maturity, the containers were inspected at one- or two-day intervals. Dead snails were removed, and each newly-laid clutch was transferred to Petri dishes in which humid conditions were maintained. Because it was not possible to attribute a clutch to a particular snail, clutches were attributed to the number of snails in each group alive at the time of the first laying, and the day of their discovery and transfer was recorded. Where more clutches were deposited than there were mothers available, we estimated the minimum number of snails that must have laid more than one clutch.

Among the clutches transferred, the fertility (proportion of eggs hatching), time for the first emergence of hatchlings and their number of whorls were recorded. Hatching was asynchronous and the hatchlings were transferred as they emerged.

We defined the reproductive lifespan as the time that elapsed between the production of the first and last clutch in each group, the post-reproductive lifespan as the period between the last reproduction and the death of the last survivor in each group, and the adult lifespan as the period from a snail's first reproduction to death. All of these parameters were calculated based on the offspring generation raised in the groups. The following life history traits were recorded: clutch numbers and size, number of eggs per individual based on the number of adult individuals alive at the time of laying (fecundity), and hatching success (fertility) in the clutches laid and removed. Survival was recorded at monthly intervals over the whole period, whether the snails were juvenile or adult.

The programme for *T. striolatus* was started in July 2018, and that for *X. erjavecii* began in June 2019. While the mortality and clutch-laying were recorded to within a few days once the snails had become

adults, we presented the data in terms of months since the start of the programmes. Thus, the pre-reproductive phase is the number of months before that in which the first clutch was found; the reproductive phase includes the months in which both the first and last clutches were found; and the post-reproductive phase is that from the first month following that in which the final clutch was laid to the last month in which any snail remained alive.

While the data for some features of the life history was both relatively consistent and normally distributed, many aspects were very variable within species. We have treated the groups as replicates, using medians rather than means, and testing for differences between species by non-parametric methods, most often by employing the Mann-Whitney U test ([Zar 2010](#)). Values of U, the test statistic, were used to calculate z, the normal deviate, to estimate the probability that two data sets had the same median value. The statistical analyses were conducted using STATISTICA software, version 13.1 (StatSoft).

Data on the raw reproductive features of *X. erjavecii* and *T. striolatus* in each group of snails in which reproduction occurred is provided as Supplementary Material (SM.01).

Results

No snail reared singly laid any clutches; thus, uniparental reproduction appears not to happen. The patterns of growth and mortality were broadly the same as for those raised in groups (SM.01), and they are not considered any further.

Despite some differences among the groups (SM.01), there were clear and consistent differences between the two species. Growth rates, measured as the number of whorls, were initially rapid, but slowed, effectively to zero, at the time of the first clutch deposition (Fig. 2; SM.01). *X. erjavecii* grew faster than *T. striolatus*; likewise, both the first recorded clutch and the median first clutch were recorded earlier in *X. erjavecii* (see below).

The pattern of mortality also differed between the species (Fig. 3). *T. striolatus* suffered high levels of mortality in the first few months but then had a long period in which the mortality was very low, only increasing at about three years of age. *X. erjavecii* suffered a lower level of early mortality, but showed a steady loss rate thereafter, meaning that its overall survival was less than *T. striolatus* after about two years. The oldest *T. striolatus* lived for 1589 days (four years and four months), while for *X. erjavecii* the figure was 1288 (three years and six months).

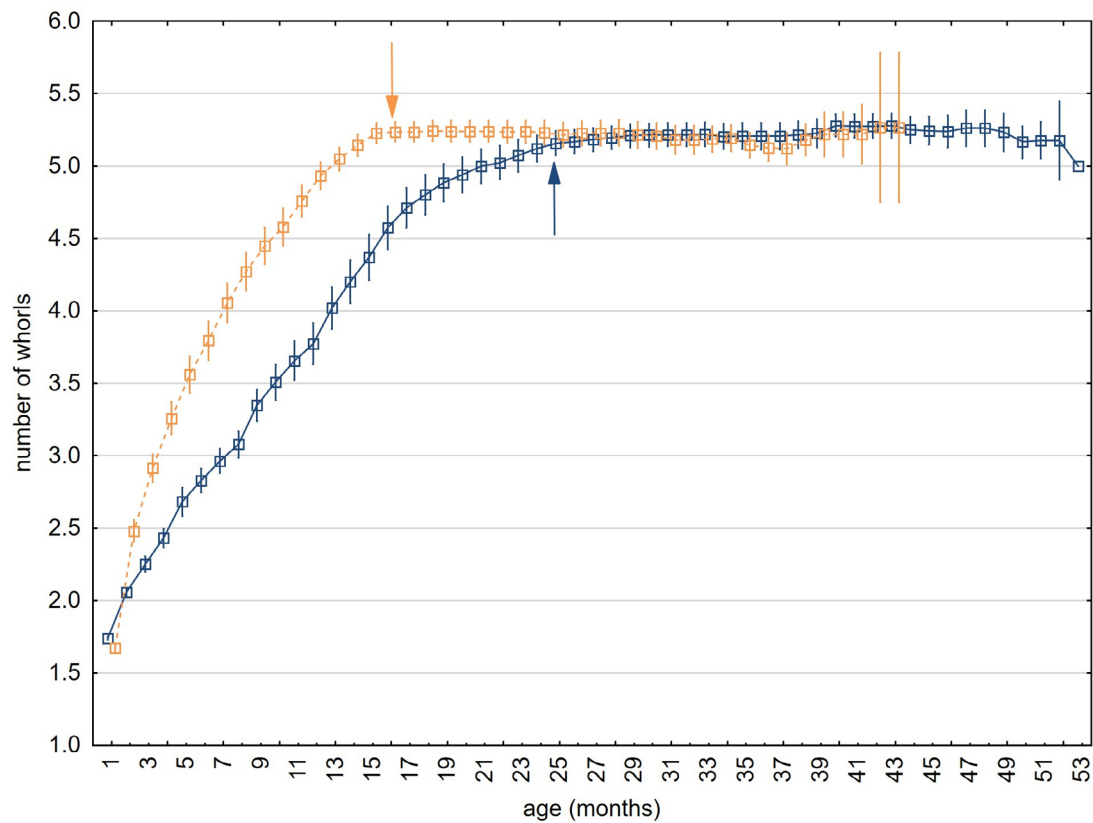


Fig. 2. Growth patterns of *T. striolatus* (n = 150, blue) and *X. erjaveci* (n = 150, orange). Arrows indicate the first clutch. The error bars represent 95% confidence intervals.

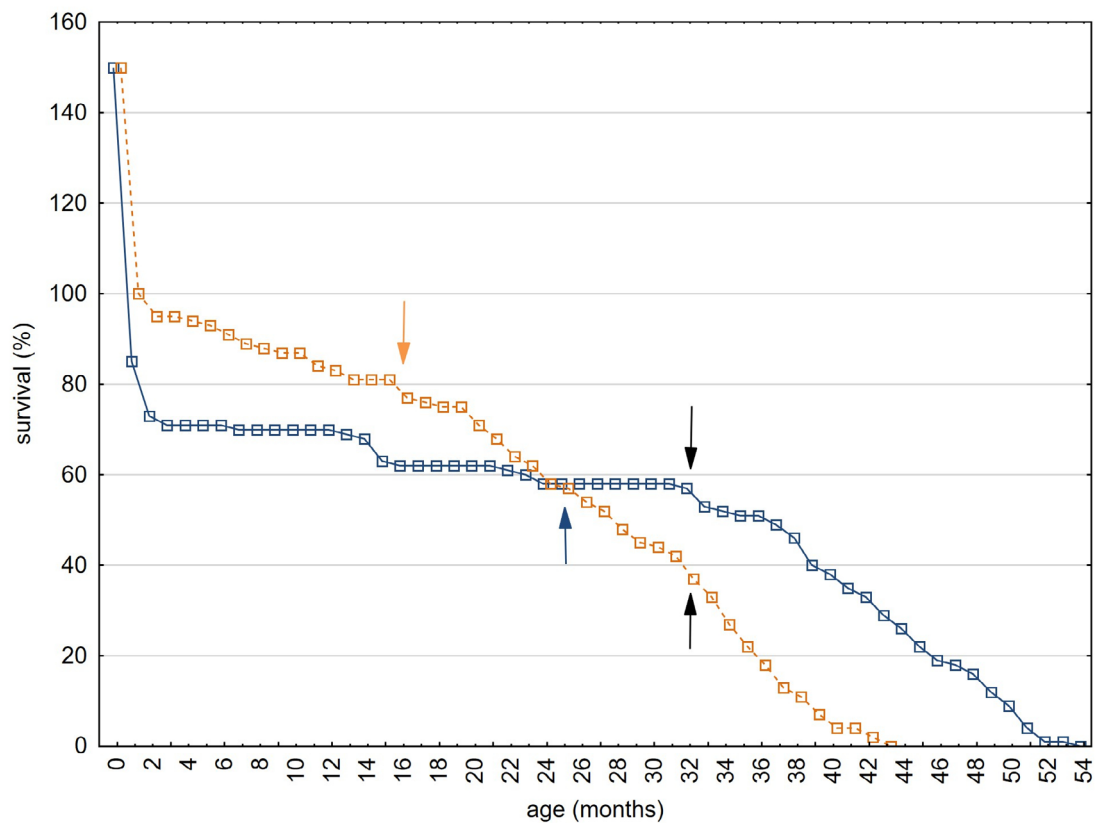


Fig. 3. Temporal trends in the survivorship of the F1 generation in *T. striolatus* (n = 150, blue) and *X. erjaveci* (n = 150, orange). Arrows indicate: median first clutch time in *T. striolatus* (blue) and *X. erjaveci* (orange); last clutch (black) in both species.

Some morphological features, such as the egg size, as well as the number of whorls at hatching and at adult size, were both very similar between the species and relatively constant (Table 1), as was the time to hatching. There were no significant differences based on t tests.

However, there were great differences among the groups within species and the distributions were

usually far from normal. We use the groups as replicates to compare the two species (SM.01; Table 2). All groups of *X. erjavecii* produced some clutches, but only nine of *T. striolatus* did so, and we used only these in our comparisons. The remaining six showed a pattern of mortality very similar to those that were fertile.

Table 1

Details of the morphological characteristics and time to hatching in *T. striolatus* and *X. erjavecii*, with the SD and ranges in parentheses. The eggs are slightly ovoid. For the egg size, n represents the numbers as measured in clutches that were removed as they were laid. All 180 (groups and the singly reared) hatchlings were measured as they were allocated. 23 (*T. striolatus*) and 80 (*X. erjavecii*) snails that reproduced (mothers) were available. 38 and 156 successful clutches were examined

	<i>T. striolatus</i>	n	<i>X. erjavecii</i>	n	p
egg size (mm)	1.3×1.4 ± 0.1 (1.1-1.5×1.2-1.6)	100	1.2×1.5 ± 0.2 (1-1.5×1.4-1.6)	100	n.s.
hatchlings (no. of whorls)	1.7 ± 0.08 (1.5-2)	180	1.65 ± 0.2 (1.4-2.1)	180	n.s.
size at first egg-laying (no. of whorls)	5.2 ± 0.24 (4.8-5.9)	23	5.19 ± 0.3 (4.1-5.75)	80	n.s.
time to hatching (days)	16.89 ± 4.03 (11-27)	38	17.08 ± 3.32 (12-25)	156	n.s.

Table 2

Summary data on the life history parameters in the two species (SM.01 gives the results for each group reproducing). Both the mean and median eggs/clutch are given for *X. erjavecii*, as the medians on the very small number of instances that occurred in some *T. striolatus* groups were not meaningful. Max mothers: the number of adult snails to which clutches could be attributed; clutches per mother: a simple division. As fractional clutches are impossible, the 'at least one snail' row shows the minimum number of clutches necessarily produced by at least one snail. Figures in the first clutch, last clutch and last snail rows refer to the month of observation; the last three rows: pre-, reproductive and post- are the durations in months. Mann-Whitney tests show the values of z, the normal deviate and the associated probability (two-tailed) that the medians are the same

Feature	<i>X. erjavecii</i>		<i>T. striolatus</i>			
	median	range	median	range		
clutches	13	6-45	5	1-18		
eggs	411	75-932	74	11-473		
mean eggs/clutch	26.2	12.5-49	14.8	5-30.4		
median eggs/clutch	21	14-42	n/a	n/a		
max mothers	5	2-8	2	1-7		
clutches/mother	2.8	1-5.65	1.5	1-9		
at least one snail	3	1-6	2	1-9	Mann-Whitney	
eggs/mother	100.8	12.5-139	21	7.5-236.5	z	p
first clutch	16	13-21	25	20-44	3.9	0.0001
last clutch	32	20-40	32	22-44	n.s.	n.s.
last snail	39	25-43	50	43-54	3.96	0.00007
pre reproductive	15	12-20	24	21-43	3.9	0.0001
reproductive	14	7-25	5	1-10	3.78	0.00016
post reproductive	7	2-14	24	6-30	2.89	0.004
clutches followed	161		49			
% total failure	3.1		22.4			
median hatching success	50%	0-100%	24%	0-95%	3.52	0.0004
median time to hatching (days)	17	12-25	16	11-27	n.s.	n.s.

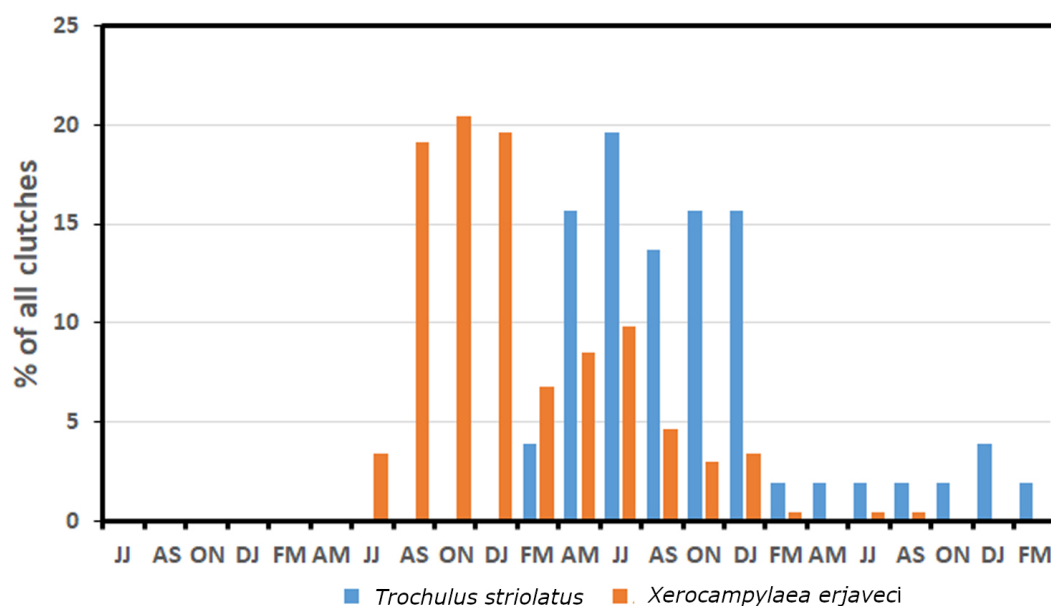


Fig. 4. The proportion of all clutches laid in bimonthly intervals from the start of the experiment, which was July 2018 for *T. striolatus* (blue) and June 2019 for *X. erjavecii* (orange).

An inspection of the data (SM.01; Table 2) shows that the reproductive success in *T. striolatus* was very variable, with one group (8) greatly outperforming all the others despite including only two possible mothers. Thus, while *X. erjavecii* tends to lay more clutches and to have more eggs in each clutch than *T. striolatus*, there was an overlap, so we are unwilling to draw conclusions (see the Discussion below). In both species, there is clear evidence that some snails lay more than one clutch. This (with the notable exception of Group 8 for *T. striolatus*) was more frequent in *X. erjavecii*. Even so, the numbers of clutches and the available mothers demonstrate that some snails in both species laid more than five clutches during the course of the investigation.

X. erjavecii starts breeding earlier than *T. striolatus* (Fig. 4). The reproductive period is also longer in *X. erjavecii* (Table 2), and there are highly-significant differences between the species in most aspects of the timing and duration of their life history. In both, however, the great majority of clutches are laid within a year of the first to be laid, although a few are laid up to two years later. There is little sign of seasonal variation in laying, with many being deposited in midwinter. In addition, the post-reproductive period is much longer in *T. striolatus* than in *X. erjavecii*.

Discussion

While complete, integrated, field studies of life histories and population dynamics can be carried out for terrestrial vertebrates (a classic example is

given by Southern 1970), determining some aspects of the reproduction and mortality trends for most invertebrates requires laboratory studies. Not only can it be hard to extrapolate from these to wild populations, but severe practical difficulties are often encountered. Hence, we have insufficient knowledge of many aspects relating to the life histories of terrestrial gastropods, although Heller (2001) and Kračmarenko (2013) have summarised what is known about the egg and clutch sizes in a wide range of species.

Beyond this basic data (which in itself reveals a great deal of variation within species), the patterns of growth and mortality among juveniles, and the fecundity of adults are far harder to determine. Not only are such studies time-consuming, but it has often proved hard to establish conditions in which successful reproduction will happen (Cain 1959; Chatfield 1968; Falkner 1973). While some species, such as *Cornu aspersum* (O. F. Müller, 1774) and *Cepaea nemoralis* (Linnaeus, 1758), can be easily reared, others, even those that are abundant and widespread in nature, prove to be more difficult (Proćków *et al.* 2013; Kuźnik-Kowalska *et al.* 2020, 2021). It is only rarely that something approaching a full account has been obtained, as in the masterly work of Myzyk (2011) on the tiny *Vertigo* species.

In considering these results, it should be noted that the laboratory conditions were maintained at a constant temperature and daylength regime over several years, thus eliminating environmental cues that might trigger behavioural and physiological re-

sponses. Our results should therefore be interpreted with care. There was a great difference in the reproductive success of the two species, despite the same, albeit artificial, conditions being applied to each. However, it seems improbable that this reflects the situation in nature, the more so as *T. striolatus* is the more widespread species, and is quick to occupy anthropogenic habitats. There are, nonetheless, similarities and differences between the two that reflect what may happen in nature. While the juvenile mortality is high in both species (greater in *T. striolatus*), which is a common feature for most land snails, the pattern of mortality in adulthood is different, as is the rate of growth before adulthood is achieved. *T. striolatus* grows more slowly, taking around two years to reach maturity; in the laboratory conditions, it survived much better in the adult form, and had a long and inexplicable period of post-reproductive life. These differences contrast with the great similarity in the size of the eggs, as well as the considerable overlap in the clutch sizes and hatching success.

In this context, our results also have a bearing on the issue of breeding systems, semelparity or iteroparity (Stearns 1992). Strictly semelparous species, including many invertebrates with a large reproductive capacity and low parental input into each egg, reproduce within a single year and die shortly thereafter (e.g. Øystein & Ejsmond 2018). Unlike *Vitrina pellucida* (O. F. Müller, 1774) (Umiński & Focht 1979) or *Theba pisana* (O. F. Müller, 1774) (Cowie 1984) that follow this pattern, these species breed in more than one year, at least under laboratory conditions. They are also capable of laying several clutches (five or more) before dying. In addition, there is also a prolonged post-reproductive period, most evident in *T. striolatus*, which is an apparently wasteful phenomenon unless, in the wild, there are chances to continue breeding.

While the absence of seasonal cues may have been significant here, it emphasises the rather fuzzy boundary between the two breeding systems and it reflects the findings of field studies on other notionally semelparous snail species (Staikou & Lazaridou-Dimitriadou 1990; Proćków *et al.* 2013; Nyumura & Asami 2015). Such flexibility is often interpreted as a bet-hedging strategy, by spreading the risk of uncertain environmental conditions across different phenotypes adapted to different environments (Hopper 1999; Solopova *et al.* 2014). Models predict that bet-hedging is more advantageous when the environment varies spatially rather than temporally, and infrequently rather than frequently. It is also more effective for a population in the process of colonising a new territory (Villa Martín *et al.* 2019). Our

experimental design cannot determine these issues, and it is hard to conceive of a laboratory design that could do so.

It is pertinent to examine the extent to which phylogenetic constraints affect variations in life history traits. In this case, we can compare our results with those obtained for *Trochulus hispidus*, a very close relative of *T. striolatus* (Proćków *et al.* 2013; Proćków & Kuźnik-Kowalska 2016). While there are great similarities in the egg size, number of whorls at hatching, clutch size and the incubation period (Table 3) among all three species, in other respects *T. hispidus* shows similarities with one or the other, depending on which measurement is being made. It appears to be more strictly semelparous than either of the other species, with a shorter reproductive period and lifespan, although some individuals live for two years and might reproduce in a second year, a conclusion that is supported by a very limited set of data from the wild (Cameron 1982). The same appears to be true of the more distantly-related hygromiid *Monacha cantiana* (Montagu, 1803) (Chatfield 1968). Nonetheless, studies on more hygromiid species are needed to investigate the degree of phylogenetic conformity. In some families such as the Clausiliidae (Sulikowska-Drozd 2009; Maltz & Sulikowska-Drozd 2014) there is some conformity, complicated by viviparity in some species, but in others, such as the Achatinidae, closely-related species show radically-different reproductive strategies (Nisbet 1974).

While caution is certainly needed in drawing conclusions from laboratory cultures, it is apparent that, as in other taxa, land snails cannot be divided neatly into semelparous and iteroparous species, and still less into those that following r or K life cycle strategies, a paradigm that has been replaced by a more sophisticated approach that considers the selective pressures on different stages in the life cycle (Reznick *et al.* 2002). In our study, two species with some phylogenetic affinity and an outwardly similar range of habitats showed differences in the patterns of growth, adult mortality and the reproductive output, while having egg and clutch sizes that were similar. Given their longevity, we can also speculate that the timing and output of reproduction is variable, and can adjust to the environmental variation and achieved body size. Significant positive or negative relationships between body size and egg production exist in different invertebrates including butterflies (Bauerfeind & Fischer 2008), decapods (Muiño 2002) and snails (Norton & Bronson 2006). In our study, all three snail species, namely *X. erjavecii*, *T. striolatus* and *T. hispidus*, produced very similar

Table 3

Comparative mean data and SD for *T. striolatus*, *T. hispidus* and *X. erjavecii*, expressed in the form used by Proćków *et al.* (2013) and Proćków & Kuźnik-Kowalska (2016) in their studies of *T. hispidus*. Lifespan is the total (mean) only for those that were alive at 300 days, roughly the time at which the first *T. hispidus* matured

Feature	<i>T. striolatus</i>	<i>X. erjavecii</i>	<i>T. hispidus</i>
egg size (mm)	1.3×1.4 ± 0.1	1.2×1.5 ± 0.2	1.5 ± 0.1
hatchling whorls	1.7 ± 0.1	1.65 ± 0.2	1.5 ± 0.2
sexual maturity (first oviposition) (days)	761.7 ± 177.6	457.1 ± 75.8	570 ± 145.4
number of eggs/mother (fecundity)	43.1 ± 64.4	78.7 ± 42	34 ± 25.7
duration of oviposition (reproductive span) (days)	279.9 ± 175	391 ± 128	103 ± 98
clutch size	20.3 ± 13.3	25.3 ± 15.9	23.7± 16.6
time to hatching (days)	16.9 ± 4	17.1 ± 3.3	13.9 ± 5.1
hatching success (fertility) (%)	37.5 ± 29.6	50.4 ± 22.3	84.6 ± 21.7
survival until age of 300 days (%)	39.4 ± 13.9	48.3± 22.8	25.3 ± 27.8
lifespan of survivors (days)	1161.9 ± 334	921.4 ± 209	775 ± 133.2

sizes of eggs, clutches and hatchlings (expressed as the number of whorls) (Table 1). Since they are hermaphrodites, in order to confirm or reject a direct relationship between an individual's body size and its egg production, a different study design would be required. However, considering the plasticity in their intraspecific shell size variation (Proćków *et al.* 2017, 2019, 2022), such a correlation may not be excluded. At least two of the species considered here, *T. striolatus* and *T. hispidus*, have existed in fluctuating climates since the Pleistocene (Harzhauser & Neubauer 2021). They are known to inhabit a very wide range of habitat conditions across their distribution ranges and are able to persist in locally variable environments (Proćków 2009; Proćków *et al.* 2017, 2014, 2022; Duda *et al.* 2011).

Author Contributions

Research concept and design: E.K.-K., M.P.; Collection and/or assembly of data: E.K.-K., M.P.; Data analysis and interpretation: E.K.-K., R.A.D.C., M.P.; Writing the article: E.K.-K., R.A.D.C., M.P.; Critical revision of the article: E.K.-K., R.A.D.C., M.P.; Final approval of article: E.K.-K., R.A.D.C., M.P.

Conflict of Interest

The authors declare no conflict of interest.

Supplementary Materials

Supplementary Materials to this article can be found online at:

<http://www.isez.pan.krakow.pl/en/fovia-biologica.html>

Supplementary files:

SM.01. Raw reproductive features of *X. erjavecii* and *T. striolatus* in each group of snails in which reproduction occurred.

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