

This article was downloaded by: [Vrije Universiteit Amsterdam]

On: 26 January 2015, At: 08:15

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Invertebrate Reproduction & Development

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tinv20>

Influence of season, temperature, and photoperiod on growth of the land snail *Helix aperta*

Saida Benbellil-Tafoughalt^a & Joris M. Koene^b

^a Laboratory of Ecology and Environment, Faculty of Nature and Life Sciences, University A. Mira of Bejaïa, 06000 Bejaïa, Algeria

^b Faculty of Earth and Life Sciences, Department of Animal Ecology, VU University, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands

Published online: 22 Jan 2015.



[Click for updates](#)

To cite this article: Saida Benbellil-Tafoughalt & Joris M. Koene (2015) Influence of season, temperature, and photoperiod on growth of the land snail *Helix aperta*, *Invertebrate Reproduction & Development*, 59:1, 37-43, DOI: [10.1080/07924259.2014.996300](https://doi.org/10.1080/07924259.2014.996300)

To link to this article: <http://dx.doi.org/10.1080/07924259.2014.996300>

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at <http://www.tandfonline.com/page/terms-and-conditions>

Influence of season, temperature, and photoperiod on growth of the land snail *Helix aperta*

Saïda Benbellil-Tafoughalt^{a*} and Joris M. Koene^b

^aLaboratory of Ecology and Environment, Faculty of Nature and Life Sciences, University A. Mira of Bejaïa, 06000 Bejaïa, Algeria;

^bFaculty of Earth and Life Sciences, Department of Animal Ecology, VU University, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands

(Received 10 July 2014; accepted 3 December 2014)

Growth strategies are often plastic and influenced by environmental conditions. Terrestrial gastropods are particularly affected by seasonal and climatic variables, and growth rate and size at maturity are key traits in their life history. Therefore, we investigated juvenile growth of *Helix aperta* snails under four combinations of temperature and photoperiod using two sets of young snails, born in the laboratory from adults collected in either the autumn (aestivating snails) or spring (active snails). Parental snails were collected from Bakaro (Northeastern Algeria). Higher temperature increased adult size and reduced the time to first reproduction. Long day photoperiod also increased the final body weight, but had no effect on the length of the growth period. The season of birth had significant effects on length of the growth period and weight of hatchlings, whereas this weight difference disappeared by adulthood. The Spring snails took less time to develop and reached similar adult body weight as the Autumn snails. These differences may be owing to differences in egg size or quality between the snails from different seasons. More rapid growth in Spring snails results in larger snails entering aestivation, a period with size-related mortality in this species.

Keywords: growth; *Helix aperta*; photoperiod; temperature

Introduction

Development time, growth, and adult size are three important life history traits. Many studies have shown that plasticity in these traits is common (e.g. Nylin 1992; Nylin et al. 1993; Cushman et al. 1994). In many species, this plasticity in growth strategy is influenced by time constraints that are caused by seasonality. Theoretical models of adaptive growth in seasonal environments indicate that when the time horizon for growth decreases, the juvenile period typically becomes shorter, and that this is often associated with a higher juvenile growth rate and a smaller size at maturity (Ludwig & Rowe 1990; Houston et al. 1993; Werner & Anholt 1993).

To survive the winter, most temperate ectotherms have to reach a certain developmental stage or a minimum body size before the onset of harsh conditions. In these species, life history analysis of the optimal age and size at maturity predicts that growth and developmental strategies should covary with time horizons for growth (Rowe & Ludwig 1991; Abrams et al. 1996; Abrams & Rowe 1996). Abrams et al. (1996) treated juvenile growth rate as an adaptively flexible trait that juveniles can adjust depending on the situation. The authors showed that there is a trade-off between growth and mortality rates, as well as a cost of maturing at a suboptimal time of year.

One group of animals that is particularly affected by the factors outlined above is terrestrial gastropods. In these animals, the determination of growth and reproduction is closely linked to the action of environmental factors on physiology. The detection of these environmental factors influences physiology and affects growth and/or reproduction (Gomot-de Vaufléury 2001). For example, Lazaridou-Dimitriadou and Sgardelis (1997) have shown that discontinuities in growth rates and population dynamics between seasons may be attributed to environmental constraints. In addition, helicid snails are generally very sensitive to thermal and hygrometric changes (e.g. *Helix aperta*: Charrier & Daguzan 1980; Chevallier 1982). According to Sacchi (1955, 1958), when temperatures are incompatible with activity (below 7 °C or beyond 27 °C), or when relative humidity (RH) is outside its optimum (75–95%), the snails become inactive and live in a state of metabolic slowdown, i.e. enter endogenous aestivation or hibernation (e.g. *Helix aspersa* and *H. aperta*: Herreid 1977; Barnhart & MacMahon 1987; Bailey & Lazaridou-Dimitriadou 1991).

The hermaphroditic land snail *H. aperta* is a “burrowing snail”, coming up above ground only during rainy weather; during dry conditions, it burrows 7–15 cm deep into the ground and aestivates by closing off its shell with a thick whitish epiphragm until rain softens

*Corresponding author. Email: tafoughalt19@yahoo.fr

the soil. Hence, this species' functioning is highly influenced by seasonal variation. For example Giusti and Andreini (1988) reported that individuals of this species, collected close to Orbetello and Castelnuovo Berardenga (respectively, Tuscany and Sienna, Italy) and maintained under laboratory conditions, reproduce preferentially in autumn from early October to mid-December. In addition, Tafoughalt-Benbellil (2010) observed egg size variation among *H. aperta* collected in September from Bakaro (Bejaïa, eastern Algeria) and kept under controlled conditions. Tafoughalt-Benbellil et al. (2011) have investigated the reproductive timing of *H. aperta* under laboratory conditions using two sets of adult snails, all collected as adults in either February or March. This species reproduced very little during winter and spring and seemed better adapted to reproduction in autumn. In addition, the authors reported that the mean egg weight was significantly heavier, and the clutch size significantly reduced, in snails sampled in March than those collected in February. Similarly, the authors observed a significant difference between autumn and spring egg size (see Tafoughalt-Benbellil et al. 2011).

To explore the importance of egg size, the present study explores the difference in hatchling size between eggs deposited in autumn and in spring by *H. aperta*. Moreover, we test experimentally how different combinations of temperature and photoperiod affect juvenile growth up to adulthood. Thus, we address whether there is a difference in quality between eggs laid in different seasons as well as whether light regime and temperature play an important role.

Methods

We used newly hatched snails of *H. aperta* Born (1778) (= *Cantareus apertus* Born 1778). This gastropod is native to the Mediterranean basin, where it is found in France, Italy, Turkey, Cyprus, and North Africa (Kerney & Cameron 1979; Schütt 2001).

The growth experiments were all performed under artificial climatic conditions using the "soilless" breeding technique developed by Daguzan (1981; see also Enée et al. 1982; Laurent et al. 1984; Gomot & Deray 1987). This technique is used in heliciculture to raise another helicid snail, *Cornu aspersum*, a ubiquitous species living beside *H. aperta* in Algeria.

Two 2.5 × 4.0 × 5.5 m rooms were used for the experiments, one at 20 °C and the other at 15 °C. The temperatures were controlled by means of 12,000 BTU air conditioners (Samha, Setif, Algeria). In each room, an opaque screen separated the two photoperiods used (16hL:8hD and 8hL:16hD, in hours (h) of light (L) and dark (D)). The lighting was provided using daylight type neon, with an intensity of 50–100 lux. The neon lamps

were connected to an electronic chronometer set to automatically control the photoperiod. In both rooms, the RH was set at 90 ± 5%.

All the experimental snails were housed in 9 × 20 × 20 cm polythene containers with a surface of 400 cm². The containers had perforated lids with 10 holes of 1 mm diameter to provide ventilation. A wet absorbent paper was placed on the floor of the containers to maintain humidity.

The growth study was conducted on two samples of young snails born in the laboratory, under controlled experimental conditions (20 °C, long-photoperiod 16 h light: 8 h dark, 90 ± 5% RH), but coming from different parents. For the first sample, aestivating parents were collected from nature in autumn (third week of September 2011) while for the second sample the parents were collected from nature in spring, at the end of hibernation (fourth week of March 2011). For both samples, the parents were immediately allowed to reproduce under the controlled experimental conditions mentioned above. To ensure the genetic identity of the two batches, all the snails were collected from Bakaro 22 km east of Bejaia in the Kabylie region (Northeastern Algeria; Latitude: 36° 65' 46.49" N Longitude: 5° 19' 13.83" E).

For each sample, four groups of newly-hatched snails, coming from 20 mixed clutches, were randomly chosen, weighed, and then placed in the transparent polystyrene containers described above. The number of newly-hatched snails was 25 per group for Spring snails and 30 per group for Autumn snails. The density in the rearing containers was 500 snails m⁻² during the first four weeks (20 newly hatched snails/container) and then 100 snails m⁻² (four newly hatched snails/container) for the following weeks of growth. The groups are coded Autumn 20 16L:8D, Autumn 15 16L:8D, Autumn 20 8L:16D, and Autumn 15 8L:16D (all produced by parents collected in autumn), and Spring 20 16L:8D, Spring 15 16L:8D, Spring 20 8L:16, and Spring 15 8L:16D (all produced by parents collected in spring).

Throughout the experiment, the animals were fed with the commercial product "*Helixal*" (Etablissements Chays, France) developed by Gomot-de Vaufleury (2000). To nourish the snails, 50 g of food was provided in each container on Petri dishes. Three times a week, at the same time, the containers were cleaned, the food renewed, and the absorbent paper changed. The boxes' locations were changed every day in the rearing room. During the total duration of the experiment, every week, all the snails were weighed individually (±0.01 g) until the onset of mating, indicating the start of the reproduction phase (in *H. aperta* species, the cessation of growth is not marked by shell-lip formation like in *C. aspersum*; Tafoughalt-Benbellil et al. 2009). For each snail, it was observed that the end of growth coincided with the first

time mating, defined as the onset of reproduction. Each week, the number of dead animals in each group was monitored during the whole experiment.

For convenience, in the rest of the paper, snails produced by parents collected in autumn and those produced by parents collected in spring will be called, respectively, Autumn snails and Spring snails.

The data were analyzed using Statistica 5.5 (StatSoft Inc. 1999). The weights of snails of the different groups were expressed as means \pm standard deviation ($M \pm SD$). The effect of temperature and light regime and their interaction on the weight of snails at reproduction were tested using two-way ANOVA. The differences between the mean weights of snails, born in different seasons, at the start of the experiment as well as the differences in the length of the growth period among the different treatments were tested using *t*-test.

A comparison between proportions test was used to compare the mortality percentages reported in the results.

To estimate growth rate, we fitted Von Bertalanffy growth curves to the data using the formula:

$$s(t) = s_0 s_a / ((s_a - s_0)e^{-rt} + s_0)$$

where *s* indicates size, *s*(*t*) size at time *t* (in weeks), *s*₀ size at time 0 (size at the start of the experiment), *s*_a asymptotic size (final size), and *r* the growth rate constant that describes how fast the organism reaches its maximum weight (Zonneveld & Kooijman 1989; Koene et al. 2008; Hoffer et al. 2012). Estimating growth rate, expressed in increment per week, allows for a direct comparison of this parameter across all the treatments and provides additional information, which is different from the measured length of the growth period.

Results

On average, the weight of newly hatched snails was 0.016 ± 0.002 mg in Autumn snails and 0.022 ± 0.002 mg in the Spring snails (see Table 1 for values for each treatment). Newly hatched snails born in spring were on average 27% heavier in terms of body weight than those born in autumn (*t*-test: *t* = 6.26; *p* < 0.01; Table 1).

The final weight of snails differed among the four groups born in autumn as well as among those born in spring (Table 1, Figure 1). The results showed that the four groups classified, in decreasing order of their final mean weight, as follows: Group 20 16L:8D, Group 20 8L:16D, Group 15 16L:8D and then Group 15 8L:16D, for the Autumn snails and Group 20 16L:8D, Group 20 8L:16D, Group 15 16L:8D, and Group 15 8L:16D for the Spring snails.

Rearing temperature and light regime had significant effects on the final weight of snails in both samples. In fact, the weight of snails at the end of the experiment

varied between groups born in the same season and reared at different temperatures (ANOVA: *F* = 27400.6; *df* = 1, 111; *p* < 0.001 for the groups born in autumn and *F* = 21856.0; *df* = 1, 91; *p* < 0.001 for the groups born in spring; the post hoc comparison showed that there is a significant difference among both groups in each sample, *p* < 0.001, Table 1, Figure 1). At 20 °C, the weight of snails was significantly heavier than at 15 °C (see Table 1).

Photoperiod affected the final weight of snails in the two seasonal groups (Table 1); long-day photoperiod snails had significantly higher body weights. Within the seasonal groups (Spring snails and Autumn snails), at 15 °C as well as at 20 °C, snails raised under the long-day photoperiod had higher body weights compared to those reared under the short-day photoperiod (ANOVA: *F* = 924.0; *F* = 1, 110; *p* < 0.001 for the groups born in autumn and *F* = 947.5; *F* = 1, 91; *p* < 0.001 for the groups born in spring, Post hoc testing revealed a significant difference, in the two samples, among the four groups, *p* < 0.001; Table 1, Figure 1).

Length of the growth period, the number of days to onset of mating, varied within and between the two seasonal groups. Rearing temperature had a significant effect on the length of the growth period (*t*-test: *t* = 9.27; *p* < 0.001; *N*₁ = 57, *N*₂ = 57 in Autumn snails and *t* = 8.72; *p* < 0.001; *N*₁ = 46, *N*₂ = 47 in Spring snails; Table 1). Snails raised at 20 °C took less time to develop than those reared at 15 °C (Table 1). In contrast, growth period did not significantly differ with photoperiod (*t*-test: *t* = 1.12.19; *p* = 0.61; *N*₁ = 57, *N*₂ = 57 in Autumn snails and *t* = 1.01; *p* = 0.53; *N*₁ = 46, *N*₂ = 47 in Spring snails; Table 1).

Overall, season of birth affected time to reproduction (*t*-test: *t* = 5.65; *p* < 0.01; *N*₁ = 114, *N*₂ = 93; Table 1). Autumn snails reached maturity and started to mate 3–4 weeks later than the Spring snails.

Regarding the difference in the final weight of snails between the seasonal groups (between Autumn and Spring snails), the results indicate that there is a small difference between the seasonal groups (Table 1). In fact, at the end of the experiment, the mean difference in adult snails is 0.1 g between Autumn and Spring snails which is only about 0.7–1.5% of adult weight.

Mortality during the experiment was low with loss of only 3.3–8% of snails in each group (Table 1). There was no significant difference within or between the two seasonal groups (Comparison between proportions test, *p* > 0.05).

Fitted growth curves of the Von Bertalanffy type on the measured body weights provided us with estimates of growth rate (*r*, Table 1). The 95% confidence intervals allow us to evaluate differences among the treatment groups, where non-overlapping confidence intervals indicate significant differences. This clearly

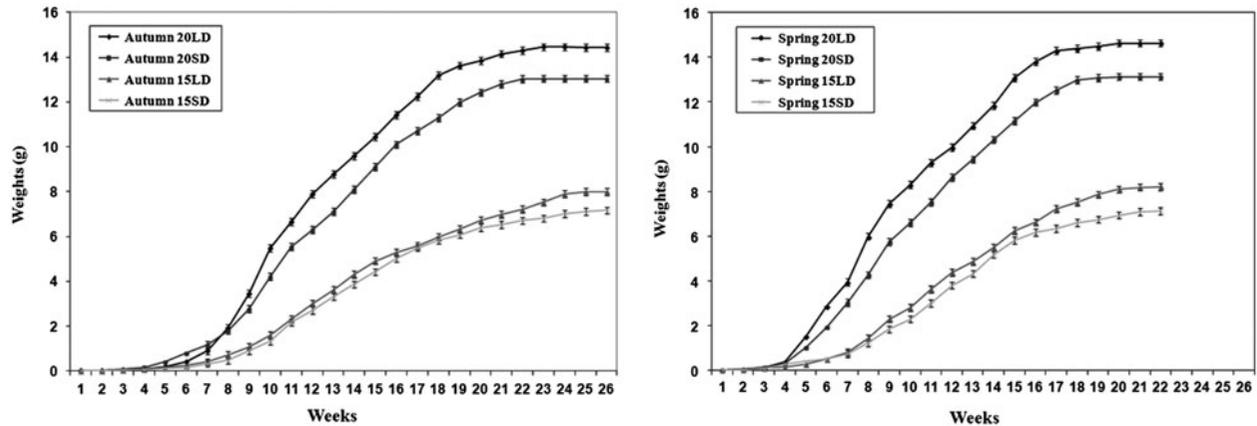


Figure 1. Weekly means and errors of body weights (g) in *H. aperta* born in autumn and those born in spring under four controlled combinations of temperature (15 or 20 °C) and photoperiod (hours of light and dark; LD, indicates long day 16L:8D; SD indicates short day 8L:16D).

Table 1. Initial and final wet weights, length of growth period, mortality rates and estimated growth rate constant of *H. aperta*, born in different seasons and reared from hatching to maturity under four combinations of temperature and photoperiod. Standard deviations are indicated behind a \pm symbol; 95% confidence intervals (for r) are indicated within brackets. Different superscripted letters indicate significant differences between the treatments based on the ANOVA results (for weight at end) and based on 95% confidence intervals (for r). The values for r are not separated by a line between Autumn and Spring because these estimates can be directly compared.

Season	Temperature (°C)	Photoperiod (Light/Dark, h)	Weight at start (g)	Weight at end (g)	Growth period (days)	Final/initial N (% died)	Estimated growth rate (r , week ⁻¹)
Autumn	20	16L:8D	0.016 \pm 0.001	14.45 \pm 0.83 ^d	160	29/30 (3.3%)	0.41 (0.40–0.42) ^b
Autumn	20	8L:16D	0.016 \pm 0.002	13.04 \pm 1.12 ^c	158	28/30 (6.7%)	0.36 (0.36–0.37) ^a
Autumn	15	16L:8D	0.016 \pm 0.002	8.01 \pm 1.11 ^b	175	28/30 (6.7%)	0.40 (0.39–0.41) ^b
Autumn	15	8L:16D	0.017 \pm 0.001	7.17 \pm 0.73 ^a	182	29/30 (3.3%)	0.46 (0.45–0.47) ^c
Spring	20	16L:8D	0.021 \pm 0.001	14.62 \pm 1.37 ^d	139	23/25 (8.0%)	0.41 (0.40–0.42) ^b
Spring	20	8L:16D	0.022 \pm 0.002	13.12 \pm 0.87 ^c	141	24/25 (4.0%)	0.40 (0.39–0.41) ^b
Spring	15	16L:8D	0.021 \pm 0.002	8.21 \pm 0.85 ^b	154	23/25 (8.0%)	0.38 (0.37–0.39) ^{ab}
Spring	15	8L:16D	0.021 \pm 0.003	7.14 \pm 0.81 ^a	152	23/25 (8.0%)	0.42 (0.41–0.44) ^b

reveals that there are also differences in growth rates among the treatments.

For the long day snails (16L:8D), there is no difference among the four treatments; they all fall into category b. For the short day snails (8L:16D), the Spring snails grow the same, while the Autumn snails grow significantly slower at 20 °C and significantly faster at 15 °C compared to the other treatments (Table 1).

Discussion

Temperature, season, and photoperiod affected aspects of growth in *H. aperta*. Snails reared at 20 °C were much larger and reproduced at a younger age than snails reared at 15 °C. These observations are in agreement with the results of a similar experiment performed on the 4th generation of laboratory-reared *H. aperta* snails, whose parents were originally collected in March (Tafoughalt-Benbellil et al. 2009). In that study, juvenile growth (length of the growth period and mean wet

weight of snails at adulthood) was strongly stimulated by a higher temperature (20 °C).

Adult weight is critical because it affects fecundity, and natural selection would favor earlier maturity in all thermal environments; faster growth at a higher temperature would result in a larger size at maturity (Angilletta et al. 2004). Similarly, Stearns (1992) and Roff (2002) reported that, generally, fecundity increases with increasing body size. Tafoughalt-Benbellil et al. (2009, 2011) reported that the number of eggs per clutch was very significantly related to the adult weight of *H. aperta*. Furthermore, rapid growth and larger body size are expected to be advantageous, not only in fecundity but also in other aspects of life history for many organisms (the bigger-is-better hypothesis, reviewed by Litvak and Leggett 1992; Arendt 1997; Blanckenhorn 2000). In addition, in *H. aperta*, size at first reproduction is very important, especially because this species has determinant growth; size at first reproduction is the final size (Tafoughalt-Benbellil et al. 2009).

Photoperiod (light regime) affected snail weights at the onset of reproduction. Indeed, within the same season and temperature, snails raised under long day photoperiod averaged higher body weights than those reared under short-day photoperiod. However, the photoperiod effect was less than the temperature effect. These findings are similar to those reported by Gomot et al. (1982) and by Gomot and Deray (1987) in their studies of *C. aspersum*, for which young snails exposed to long days achieved heavier body weights than those reared under short days. However, our observations are dissimilar to those made on a laboratory colony of *H. aperta* (Tafoughalt-Benbellil et al. 2009), in which photoperiod length had no effect on the final weight. To explain this difference, we hypothesize that the difference in the effect of photoperiod on the final weight of snails is the product of a physiological acclimatization to the laboratory conditions. Indeed, Madec (1988) showed that in *C. aspersum*, some environmental variation allows the animal to adapt to the new conditions either through plasticity of development or via the possibility of a physiological acclimatization of the species. In contrast to snail weight, our data showed that photoperiod length did not measurably affect length of the growth period (until maturity), which is in agreement with observations reported by Tafoughalt-Benbellil et al. (2009) for a laboratory colony of *H. aperta*.

Season of birth affected two aspects of life history: hatching weight and juvenile growth (length of the growth period) but not weight at first reproduction. The snails collected in spring laid larger eggs that resulted in heavier body weights at hatching compared to those collected in autumn.

Our findings suggest that the Spring snails, characterized by heavier hatchling weight, took less time to develop and reached a similar adult weight than the Autumn snails. Investment in eggs is known to vary in snails (e.g. Hoffer et al. 2012). Baur (1994) showed that larger eggs in *Arianta arbustorum* have higher nutrient content and snails require only a short period of growth to reach a shell diameter greater than 20 mm under natural conditions. Similarly, Sibly and Monk (1987) reported, in a grasshopper species, that a large egg can conceivably be an alternative to high growth rate or reduced adult size when short development times are important. These results are also consistent with variation in egg weights reported by Tafoughalt-Benbellil et al. (2011) for *H. aperta*. Snails living under Mediterranean climates, characterized by dry summers, prepare themselves as early as May to undergo a long aestivation that is essential to their survival. Thus, the increase in the weight of snails at hatching as well as the shortened length of the growth period, observed for the Spring snails, would affect juvenile mortality during periods of aestivation. For a better survival of a species and

maintenance of its populations during summer aestivation, the adjustment of the egg number per clutch, in Spring snails, is compensated by an increase in egg weight relative to the snails born in autumn (Tafoughalt-Benbellil et al. 2011). In contrast, winter survival for snails born in autumn is not a decisive factor for mortality in a region that has a sub-humid climate with mild winters (Emberger 1955). The temperature conditions and food availability in winter are also optimal for juvenile growth and, consequently, they would allow for better survival regardless of their size.

The trade-off between clutch size and egg weight in helioid snails with season is thus in agreement with the observations of Madec et al. (1998). In their study of the reproductive traits of the land snail *Helix aspersa maxima* from North Africa under laboratory conditions, the authors noted that second clutches were smaller than the first ones, but their eggs were heavier. This increase of egg size, prior to the timing of aestivation, was associated to a size-dependent mortality of juveniles during summer aestivation. Other Mediterranean snails, such as *Helix lucorum* (Staikou et al. 1988) and *Helix texta* (Heller & Ittiel 1990), also tend to reduce their number of eggs per clutch (to 70–80 eggs/clutch) and compensate by an increase in the weight of individual eggs. Similarly, many authors (Wolda & Kreulen 1973; Pollard 1975; Oosterhoff 1977; Peake 1978; Cain 1983; Cowie 1984; Madec et al. 1998, 2000) reported a trade-off between egg size and clutch size in autumnal clutches of helioid snails from Western Europe. In these species, the change in the trade-off between egg size and clutch size is linked to a size-dependent mortality of juveniles during winter, rather than summer, because in more northern climates, a lengthy hibernation occurs as an adaptation to low temperature.

Because snail growth varies adaptively and can be a plastic trait, another explanation for the longer growth period in Autumn snails, relative to Spring snails, is maternal effects. Such effects might be sought in inadequate provisioning of (specific) nutrients in the autumn eggs as compared to spring eggs. This may be supported by the fact that from late December to late March (winter), and early May to late September (summer) temperatures are not optimal for *H. aperta* (optimal temperatures range from 7 to 27 °C) (see Tafoughalt-Benbellil et al. 2011).

In conclusion, our results indicate that temperature, photoperiod, and season have significant effects on body growth. Snails reared at 15 °C grew slower, took more time to develop and reached a smaller adult body weight than those raised at 20 °C. Photoperiod length has significant effects on snail weight at adulthood, but not on the length of the growth period. The season of birth has significant effects on weight of hatchlings, juvenile growth rates, and lengths of the growth period, but not

on snail weight at adulthood. Seasonal differences on weight of hatchlings are significant and large, whereas this weight difference disappears by adulthood. As expected from our experiments, the shortened growth length in the Spring snails is associated with higher body weights at hatching (and is probably due to either heavier or qualitatively better eggs).

Acknowledgments

We would like to thank Pr M. Sahnoune for his help in some of the statistical analysis used in this paper. We also thank the anonymous reviewers for valuable comments.

Supplemental data

Supplemental data for this article can be accessed <http://dx.doi.org/10.1080/07924259.2014.996300>.

References

- Abrams PA, Leimar O, Nylin S, Wiklund C. 1996. The effect of flexible growth rates on optimal sizes and development times in a seasonal environment. *The American Naturalist*. 147:381–395.
- Abrams PA, Rowe L. 1996. The effects of predation on the age and size of maturity of prey. *Evolution*. 50:1052–1061.
- Angilletta MJR, Steury TD, Sears WM. 2004. Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integrative and Comparative Biology*. 44:498–509.
- Arendt JD. 1997. Adaptive intrinsic growth rates: an integration across taxa. *The Quarterly Review of Biology*. 72:149–177.
- Bailey SER, Lazaridou-Dimitriadou M. 1991. Inverse temperature acclimation of heart rate in hibernating land snails. *Journal of Comparative Physiology B*. 160:677–681.
- Barnhart MC, MacMahon BR. 1987. Discontinuous carbon dioxide release and metabolic depression in dormant land snails. *Journal of Experimental Biology*. 128:123–138.
- Baur B. 1994. Inter-population differences in propensity for egg cannibalism in hatchlings of the land snail *Arianta arbustorum*. *Canadian Journal of Zoology*. 48:851–860.
- Blanckenhorn WU. 2000. The evolution of body size: what keeps organisms small? *The Quarterly Review of Biology*. 75:385–407.
- Cañin AJ. 1983. Ecology and ecogenetics of terrestrial molluscan populations. In: Russel-Hunter WD, editor. *The mollusca*. Vol. 6. London: Academic Press; p. 597–647.
- Charrier M, Daguzan J. 1980. Food consumption: production and energy budget in *Helix aspersa* Müller (Gastropoda Pulmonata). *Annales de la Nutrition et de l'alimentation*. 34:147–166.
- Chevallier H. 1982. Facteurs de croissances chez des gastropodes pulmonés terrestres paléarctiques en élevage. *Haliotis*. 12:29–46.
- Cowie RM. 1984. The life-cycle and productivity of the land snail *Theba pisana* (Mollusca: Helicidae). *The Journal of Animal Ecology*. 53:311–325.
- Cushman JH, Rashbrook VK, Beattie AJ. 1994. Assessing benefits to both participants in a lycaenid-ant association. *Ecology*. 75:1031–1041.
- Daguzan J. 1981. Contribution à l'élevage de l'escargot Petit-gris *Helix aspersa* Müller (Mollusque Gastéropode Pulmoné Stylommatophore). II- Evolution de la population juvénile de l'éclosion à l'âge de 12 semaines en bâtiment et en conditions contrôlées. *Annales de Zootechnie*. 31:87–110.
- Emberger L. 1955. Une classification biogéographique des climats. *Travaux du Laboratoire de Botanique et de Zoologie Faculté des Sciences. Montpellier*. 7:3–43.
- Enée J, Bonnefoy-Claudet R, Gomot L. 1982. Effet de la photopériode artificielle sur la reproduction de l'escargot *Helix aspersa* Müller. *Comptes Rendus de l'Académie des Sciences Paris*. 294:357–360.
- Giusti F, Andreini S. 1988. Morphological and ethological aspects of mating in two species of the family Helicidae (Gastropoda Pulmonata) *Theba pisana* (Müller) and *Helix aperta* (Born). *Monitore Zoologico Italiano. (N.S.)*. 22:331–363.
- Gomot L, Deray A. 1987. Les escargots La Recherche. 186:302–311.
- Gomot L, Enée J, Laurent J. 1982. Influence de la photopériode sur la croissance pondérale de l'escargot *Helix aspersa* Müller en milieu contrôlé. *Comptes Rendus de l'Académie des Sciences Paris*. 294:749–752.
- Gomot-de Vaufleury A. 2000. Standardized growth, toxicity testing (Cu, Zn, Pb and pentachlorophenol) with *Helix aspersa*. *Ecotoxicology and Environmental Safety*. 46:41–50.
- Gomot-de Vaufleury A. 2001. Regulation of growth and reproduction. In: Barker GM, editor. *The biology of terrestrial molluscs*. Wallingford: CAB International; p. 331–355.
- Heller J, Ittliel H. 1990. Natural history and population dynamics of the land snail *Helix texta* in Israel (Pulmonata, Helicidae). *Journal of Molluscan Studies*. 56:189–204.
- Herreid CF. 1977. Metabolism of land snails (*Otala lactea*) during dormancy, arousal, and activity. *Comparative Biochemistry and Physiology Part A: Physiology*. 56:211–215.
- Hoffer JNA, Schwegler D, Eilers J, Koene JM. 2012. Mating rate influences female reproductive investment in a simultaneous hermaphrodite, *Lymnaea stagnalis*. *Animal Behaviour*. 84:523–529.
- Houston AI, McNamara JM, Hutchinson JMC. 1993. General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 341:375–397.
- Kerney MP, Cameron RAD. 1979. A field guide to the land snails of Britain and NW Europe. London: William Collins.
- Koene JM, Loose MJ, Wolters L. 2008. Mate choice is not affected by mating history in the simultaneously hermaphroditic snail *Lymnaea stagnalis*. *Journal of Molluscan Studies*. 74:331–335.
- Laurent J, Deray A, Grimard AM. 1984. Influence de la photopériode, du degré d'hétérogénéité de la population sur la dynamique de croissance et la maturation sexuelle de l'escargot *Helix aspersa*. *Comptes Rendus de la Société de Biologie*. 178:421–441.
- Lazaridou-Dimitriadou M, Sgardelis S. 1997. Phenological patterns and life history tactics of Helicoidea (Gastropoda, Pulmonata) snails from Northern Greece. *Iberus*. 15:25–34.
- Litvak MK, Leggett WC. 1992. Age and size-selective predation on larval fishes: the bigger-is-better hypothesis revisited. *Marine Ecology Progress Series*. 81:13–24.
- Ludwig D, Rowe L. 1990. Life-history strategies for energy gain and predator avoidance under time constraints. *The American Naturalist*. 135:686–707.

- Madec L. 1988. Origine et importance des différences affectant la forme et la taille des œufs chez l'escargot "Petit-gris" (*Helix aspersa* Müller). *Haliotis*. 19:143–152.
- Madec L, Desbuquois C, Coutellec-Vreto MA. 2000. Phenotypic plasticity in reproductive traits: importance in the life history of *Helix aspersa* (Mollusca: Helicidae) in a recently colonized habitat. *Biological Journal of the Linnean Society*. 69:25–39.
- Madec L, Guiller A, Coutellec-Vreto MA, Desbuquois C. 1998. Size-fecundity relationships in the land snail *Helix aspersa*: preliminary results on a form outside the norm. *Invertebrate Reproduction and Development*. 34:83–90.
- Nylin S. 1992. Seasonal plasticity in life history traits: growth and development in *Polygonia c-album* (Lepidoptera: Nymphalidae). *Biological Journal of the Linnean Society*. 47:301–323.
- Nylin S, Wiklund C, Wickman PO, Garcia-Barros E. 1993. Absence of trade-offs between sexual size dimorphism and early male emergence in a butterfly. *Ecology*. 74:1414–1427.
- Oosterhoff LM. 1977. Variation in growth rate as an ecological factor in the land snail *Cepaea nemoralis* (L.). *Netherlands Journal of Zoology*. 27:1–132.
- Peake J. 1978. Distribution and ecology of the Stylommatophora. In: Fretter V, Peake J, editors. *The Pulmonates*. Vol. 2A. London: Academic Press; p. 171–217.
- Pollard E. 1975. Differences in shell thickness in adult *Helix pomatia* L. from a number of localities in Southern England. *Oecologia*. 21:85–92.
- Roff DA. 2002. *Life history evolution*. Sunderland (MA): Sinauer Associates.
- Rowe L, Ludwig D. 1991. Size and timing of metamorphosis in complex life cycles: time constraints and variation. *Ecology*. 72:413–427.
- Sacchi CF. 1955. Il contributo dei molluschi terrestri alle ipotesi del "pontesiciliano". Elementi tirrenici ed orientali nella malacofauna del Maghreb. *Archivio Zoologico Italiano*. 40:49–181.
- Sacchi CF. 1958. Les mollusques terrestres dans le cadre des relations biogéographiques entre l'Afrique du Nord et l'Italie. *Vie et milieu*. 9:11–52.
- Schütt H. 2001. Die Türkische Landschnecken [The Turkish land snails]: 1758–2000. *Acta Biologica Benrodis*. 4:1–549.
- Sibly R, Monk K. 1987. A theory of grasshopper life cycles. *Oikos*. 48:186–194.
- Staikou A, Lazaridou-Dimitriadou M, Farmakis N. 1988. Aspects of the life cycle, population dynamics, growth and secondary production of the edible snail *Helix lucorum* Linnaeus, 1758 (gastropoda, pulmonata) in Greece. *Journal of Molluscan Studies*. 54:139–155.
- Stearns SC. 1992. *The Evolution of Life-histories*. Oxford: Oxford University Press.
- Tafoughalt-Benbellil S. 2010. Etude de l'influence de la durée de la photopériode et de la température sur la croissance et la reproduction des escargots de l'espèce *Helix aperta* Born (Gasteropoda, Helicidae) [Thèse de Doctorat] [Study of the influence of duration of photoperiod and temperature on the growth and reproduction of the land snail *Helix aperta* Born (Gasteropoda, Helicidae) [Doctoral thesis]]. Bejaia: Université A. Mira.
- Tafoughalt-Benbellil S, Sahnoune M, de Vaufléury A, Moali A. 2009. Effects of temperature and photoperiod on growth and reproduction of the land snail *Helix aperta* Born (Gastropoda, Pulmonata). *Revue d'Ecologie (la Terre et la Vie)*. 64:207–219.
- Tafoughalt-Benbellil S, Sahnoune M, de Vaufléury A, Moali A. 2011. Influence of sampling date on reproduction in the land snail *Helix aperta* kept under controlled conditions of temperature and photoperiod. *Revue d'Ecologie (la Terre et la Vie)*. 66:43–54.
- Werner EE, Anholt BR. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *The American Naturalist*. 142:242–272.
- Wolda M, Kreulen DA. 1973. Ecology of some experimental populations of the landsnail *Cepaea nemoralis* L. II. Production and survival of eggs and juveniles. *Netherlands Journal of Zoology*. 23:168–188.
- Zonneveld C, Kooijman SALM. 1989. Application of a dynamic energy budget model to *Lymnaea stagnalis* (L.). *Functional Ecology*. 3:269–278.