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Food intake, growth, and reproduction as affected by day length and food availability in the pond snail *Lymnaea stagnalis*⋆

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Abstract: With the aim of integrating the physiology and evolutionary ecology of *Lymnaea stagnalis* (Linnaeus, 1758), we studied the effects of day length and food availability on the energy budget. Snails were assigned to two different photoperiods and three levels of food availability. The snails were kept individually, and food consumption, growth, and egg production were measured for about 2 months. Snails could nearly compensate for a one-day starvation period by increasing the rate of food-intake. However, food-intake rates did not increase further after a starvation period of 2 days. Growth was well described by the Von Bertalanffy growth equation. The ultimate size of snails kept under medium-day conditions (MD; light:dark = 12:12 h) was not affected by food availability. By contrast, the ultimate size of snails kept under long-day conditions (LD; light:dark = 16:8 h) depended on food availability; those fed the lowest quantities grow the least. Dry-weight densities (dry weight/wet weight) of MD snails were considerably above those of LD snails. In MD snails, food availability did not appreciably affect dry-weight density. By contrast, in LD snails, dry-weight density decreased with decreasing food availability. The reproductive output of LD snails declined with declining food availability, but was 2 to 4 times that of MD snails. The difference in reproductive output was largely accounted for by the difference in stored energy, *i.e.* dry-weight density. To gauge the extent to which the conclusions from our laboratory work applied to free-living snails, a field study was conducted. The wild-caught snails' dry-weight density was also lowest in long-day conditions when most eggs were laid. However, the dry-weight densities during medium and short days were lower than the dry-weight densities of laboratory animals under LD conditions. Thus, in the field, snails stored less energy than in the laboratory.

Key words: allocation, food availability, growth, reproduction

Ecological studies on the energetic costs of growth and reproduction have far-reaching implications for understanding the functioning of animals in relation to their environment (*e.g.*, Dillon 2000). Physiological studies focus on the underlying regulatory processes of growth and reproduction. The latter approach has resulted in a vast knowledge of the basic mechanisms of regulation of growth and reproduction (reviewed in Chase 2002). However, the integration of ecological and physiological knowledge is often hampered because the choice of experimental animal is determined by several considerations that rarely coincide. As a result, few if any experimental animals exist that are thoroughly studied from both perspectives. The aim of the present paper is to fill this gap in knowledge of the physiological ecology of the pond snail *Lymnaea stagnalis* (Linnaeus, 1758).

The great pond snail *Lymnaea stagnalis* is a pulmonate gastropod belonging to the suborder Basommatophora and the family of the Lymnaeidae. This simultaneous hermaphrodite occurs commonly in European lakes, ponds, and ditches and can be easily collected in the field (*e.g.*, Puurtinen *et al.* 2004) where it has an annual life cycle. Eggs are laid in masses containing between 50 and 150 eggs, depending on the individual's body size (Koene *et al.* 2007). Offspring can be produced via self-fertilization and cross-fertilization; when allosperm has been received, there is a preference for outcrossing (Cain 1956, Knott *et al.* 2003). Large populations can also be cultured in the laboratory under semi-natural conditions (Van Der Steen *et al.* 1969). These laboratory conditions allow for extensive control over external factors (*e.g.*, food, temperature, light, etc.) as well as experimental manipulations (*e.g.*, De Visser *et al.* 1994) and neurophysiological experiments (*e.g.*, De Boer *et al.* 1997). As a result, the species has become a widely used, physiological model system for research focusing on neuronal and endocrinological control mechanisms (*e.g.*, El Filali *et al.* 2006; reviewed in Chase 2002).

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The organs and cell groups producing hormones that regulate growth (Geraerts 1976) and reproduction (Geraerts and Algera 1976, Geraerts and Bohlken 1976, De Boer *et al.* 1997) are known, as well as the amino acid sequences of these hormones (Ebberink *et al.* 1985, Vreugdenhil *et al.* 1985, Smit *et al.* 1988, De Lange *et al.* 1997, Jiménez *et al.* 2004). For example, growth is regulated by a growth hormone produced by the light green cells (LGC). Egg laying is triggered by the discharge of the neurosecretory caudodorsal cells (CDC; Ter Maat *et al.* 1989). These neurons are electrically coupled and during a discharge, a massive amount of the egg-laying hormone is released. This hormone, called CDCH, has been fully characterized (Geraerts *et al.* 1985, Jiménez *et al.* 2004) and gives rise to ovulation, which results within two hours in an egg mass being oviposited.

Despite the detailed knowledge about the neuroendocrinological regulation of growth and reproduction in this species, surprisingly little is known about the functioning of these processes in relation to the animal's environment. Environmental variables, like day length and food availability, are known to affect the allocation of energy to growth and reproduction (*e.g.*, Scheerboom 1978, Bohlken and Joosse 1982). However, no detailed studies have been performed to quantify these environmental factors. Such studies should be quite relevant for an understanding of the hormonal regulation of growth and reproduction. To bring these two fields of research closer together, in the present study we focused on the interaction between photoperiod and food availability in the allocation of energy to growth and reproduction.

MATERIALS AND METHODS

Experimental design

Two laboratory experiments were performed, one under medium-day conditions (MD: light:dark = 12:12 h; duration 80 days), the other under long-day conditions (LD: light: dark = 16:8 h; duration 57 days). The adult snails, taken from a mass culture bred under standard conditions, *i.e.*, MD (Van der Steen *et al.* 1969), were kept individually in perforated polyethylene beakers with a lid (460 ml). At the start of the experiment, the snails were adult. The shell lengths of the MD animals were 24.40 ± 1.55 mm, the LD animals 22.71 ± 0.91 mm. Group size was 20 in the MD experiment and 15 in the LD experiment. The perforated beakers were placed in a tank with continuous water exchange using Amsterdam tap water through Cu-free piping. The water temperature was kept at 17.5 ± 0.5 °C. Beakers were changed every 3 or 4 weeks. Coprophagy was not prevented.

In both experiments, three levels of food availability were studied by varying the frequency at which food was supplied. The snails in group 1 received lettuce in excess of their requirements every day, those in group 2 at two subsequent days followed by one day of starvation, and those in group 3 every third day followed by two days of starvation.

Measurements of food consumption, growth, and egg production were made. A broad-leaved variety of lettuce was used as food. From the flat parts of the leaves, where only small vascular bundles are present, circular discs were punched with a surface area of 19.6 cm^2. Snails were either provided with 2 discs or starved. After 24 h the remaining lettuce was removed from the jars, spread out on a Perspex plate, and covered with a glass plate. The plates were subsequently recorded on a video tape, and recordings were digitized to determine the surface area. The difference between the area provided and remaining was used as a measure for consumption.

Every two weeks the shell heights were measured with a caliper to the nearest 0.1 mm. At the end of the experiment, snails were frozen in liquid nitrogen. After thawing, the shell was separated from the body, and the wet weight of the body was determined. The shell and body were freeze-dried, after which they were weighed to the nearest 0.1 mg. Dry weight density (*i.e.*, the ratio of dry weight to wet weight, expressed as a percentage) was used as a measure of consumption.

Egg masses were collected every day. The egg masses were stored in 70% ethanol until the number of eggs per egg mass was counted.

Data analysis

Von Bertalanffy growth curves were fitted to the data on shell heights for individual snails. The Von Bertalanffy growth curve is given by the equation:

$$h(t) = h_e - (h_b - h_e)\exp\{-gt\} \quad (1)$$

where $h(t)$ denotes the current shell height; h_e, the ultimate shell height, which may eventually be reached if the snail is kept under constant conditions for a long period; h_b, the shell height at the start of the experiment; and g, the Von Bertalanffy growth coefficient. The use of the Von Bertalanffy curve has previously been shown to be appropriate for this species (Zonneveld and Kooijman 1989).

For regression analyses we assumed a normally distributed scatter with homogeneous variance around the model curves. Given this assumption, maximum likelihood estimates are given by the least squares method. To obtain the least squares estimates of the parameters, we used the Gauss-Newton method (Richter and Sondgerath 1990). Standard deviations of the parameters were estimated according to the large sample theory of maximum likelihood estimators (Cox

and Hinkley 1974). Comparisons between groups were made using Tukey's post-hoc test.

Field study

For nearly two years, from 29 August 2002 to 14 April 2004 we collected a total of 564 *Lymnaea stagnalis* specimens from two ditches in the Eempolder near Amsterdam, the Netherlands. The Eempolder is a protected landscape enclosed by dikes consisting of pastures separated by ditches. Samples were taken in all months of the year, and on each sampling date we tried to collect a representative sample of both adults and juveniles. Immediately after collection, the animals were weighed and shell length was measured. The snails were subsequently dissected and the shell, albumen gland, and prostate gland were removed and weighed (these data will be published elsewhere, Koene *et al.*, unpubl. data). The soft body parts were freeze dried and weighed. All animals were checked for parasites. All year round, almost 50% of the snails collected in the field are infected with one or more species of parasites, among which were *Trichobilharzia ocellata, Echinostoma revolutum*, *Opisthioglyphe ranae*, *Hypoderaeum conoidum*, *Diplostomum spathaceum*, and *Pseudoechinoparyphium echinatum* (Loy and Haas 2001, De Jong-Brink and Koene 2005, Koene *et al.*, unpubl. data). In the current paper we present data on the dry weight density of individuals not containing parasites ($N = 283$).

RESULTS

Growth and food availability

Von Bertalanffy growth curves were fitted to the measured shell heights (Table 1). The growth rate parameter g in equation 1 is a measure for the curvature of the growth curve. If the time constant g^{-1} is larger than the duration of the experiment, the curvature will be barely observable; hence, it can be very difficult to estimate this parameter. This situation applied to only 7 MD snails of group 3, which were the slowest growing snails. Standard deviations are based on the estimates of the parameters for the individual snails.

Table 1. Means (and standard deviations) of parameter estimates of Von Bertalanffy growth curves. Abbreviations: h_e, ultimate shell height; h_b, initial shell height; g, the Von Bertalanffy growth coefficient; *n*, sample size.

Day length	Food regimen	h_e (SD) cm	h_b (SD) cm	g (SD) d^{-1}	*n*
MD	1	3.45 (0.22)	2.25 (0.20)	0.0394 (0.018)	20
	2	3.53 (0.28)	2.25 (0.17)	0.0284 (0.0077)	20
	3	3.43 (0.53)	2.25 (0.18)	0.0145 (0.0050)	13
LD	1	3.33 (0.29)	1.86 (0.12)	0.0493 (0.014)	15
	2	3.35 (0.27)	1.99 (0.084)	0.0321 (0.010)	15
	3	2.62 (0.18)	2.03 (0.12)	0.0307 (0.011)	15

The growth coefficient g was significantly affected by day length and food availability (two way ANOVA; day length: $F = 15.6$, $df = 1, 92$, $P < 0.001$; food availability: $F = 25.4$, $df = 2, 92$, $P < 0.001$), but there seemed to be no interaction between these two factors ($F = 2.0$, $df = 1, 92$, $P = 0.14$). The growth coefficient was larger in LD snails than in MD snails, indicating that the LD animals grew faster. The growth coefficient decreased with decreasing food availability. In LD conditions, the animals had slower growth. Also, limited food supply led to slower growth rates.

Food availability had no effect on the ultimate length in MD snails (one way ANOVA, $F = 0.28$, $df = 2, 50$, $P > 0.5$). In LD snails, food availability also had no effect on the ultimate lengths of groups 1 and 2, but snails in group 3 remained much smaller ($P < 0.001$). The ultimate shell heights of groups 1, 2, and 3 of MD snails differed slightly from those of group 1 and 2 of LD snails (one way ANOVA, $F = 5.6$, $df = 1, 68$, $0.01 < P < 0.05$). In conclusion, when food was abundant, day length had a small effect on the ultimate size attained, even though this length was reached later by LD animals. However, when food was limited, LD animals grew more slowly and reached a smaller ultimate size.

Dry weights consist of structural body mass and stored energy. The dry weight density, *i.e.*, dry weight per wet weight (without shell), can be used to compare the amounts of stored energy in different groups. Dry-weight densities of MD and LD snails at the three levels of food availability are shown (Fig. 1A). A two-way ANOVA showed that MD and LD snails reacted similarly to food availability (interaction between day length and food availability: $F = 2.3$, $df = 2, 99$, $P > 0.05$). The MD snails had higher dry-weight densities than LD snails ($F = 293.0$, $df = 1, 99$, $P < 0.0001$). There was a significant overall effect of food availability ($F = 4.05$, $df = 2, 99$, $P < 0.05$); the lowest dry-weight densities occurred in the animals receiving the least amount of food and *vice versa* (Tukey at $P = 0.05$).

In summary, food availability determines only growth rate and not ultimate size in medium-day animals; however, under long-day length conditions, food availability was a major determinant of final size as well as growth rate. Stored energy was higher with higher food availability in both groups.

Food consumption and fecundity

At each level of food availability, the fecundity of LD animals was higher than that of MD animals. Also, when food was present on two out of three days, fewer eggs were laid on the day when no food was present. However, when

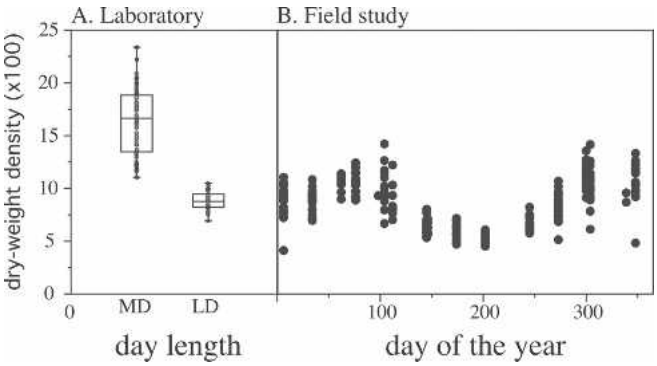

Figure 1. Dry weight densities under LD (Long Day, 16:8 h light: dark) and MD (Medium Day, 12:12 h light:dark) conditions in the laboratory and in the field. A. Laboratory snails. Data are shown for animals that received food on all days of the schedule. LD animals had lower dry weight densities than did MD animals ($P < 0.001$; Student's *t*-test). B. Dry weight densities of wild-caught snails. During the year, a minimum was reached during summer.

food was provided on one day out of three, egg production was equal (MD) or lower (LD) than on the days the animals went without food. Table 2 provides the data on consumption and oviposition on each of the three days of the food cycle. The pattern of egg production was established during the first three-day cycle and persisted throughout the experiment. In the MD experiment, 19, 17, and 10 snails of group 1, 2, and 3, respectively, produced at least 1 egg mass. In the LD experiment, all of the snails produced egg masses. The average interval between oviposition bouts depended on food availability. In LD animals, the mean intervals were 2.13 (SD = 0.26), 2.41 (SD = 0.36), and 4.18 (SD = 0.89) days for groups 1, 2, and 3, respectively. In MD animals the intervals were 9.85 (SD = 9.66), 16.77 (SD = 6.49), and 36.89 (SD = 26.35). Animals that did not lay any eggs were excluded from the analyses; this occurred only in the MD group as follows: group 1, $n = 1$ snail; group 2: $n = 2$; group 3: $n = 10$. The differences between food regimes were significant in both LD (Kruskal-Wallis, $H = 31.6$, $df = 2$, $P < 0.0001$) and MD conditions ($H = 13.7$, $df = 2$, $P < 0.001$). LD animals at all three levels of food availability laid more eggs and egg masses than their MD counterparts. These results are in keeping with earlier studies on the effects of daylength (Bohlken and Joosse 1982).

Egg masses shown in Table 2 for a certain day were collected at the end of that day of the food cycle. Snails that were fed every day (*i.e.*, group 1) showed no preference for any day of the food cycle to oviposit (MD: Chi-square, $\chi^2 = 1.46$, $P > 0.01$; LD $\chi^2 = 0.536$, $P > 0.01$). Snails of group 2 laid the fewest egg masses on the day they were starved. However, MD snails laid the most egg masses on the second day of the food cycle ($\chi^2 = 45.2$, $P < 0.01$), whereas LD snails laid the most egg masses on the first day ($\chi^2 = 57.1$, $P < 0.01$). No preference could be demonstrated for MD snails of group 3 ($\chi^2 = 1.75$, $P < 0.01$), probably due to the small number of egg masses that were laid. In LD group 3 snails, most egg masses were laid on the days they were starved ($\chi^2 = 9.66$, $P < 0.01$).

Because the data in Table 2 are not independent, the results should be interpreted with caution. Nevertheless, we think that the differences between the groups can be attributed to the food availability per se. In both groups that were fed every day there was not even a slight indication of a periodicity, whereas in all other groups the periodicity was pronounced, with the exception of MD group 3, where very few egg masses were laid. The patterns of egg laying during the three-day cycle did not change during the experiment.

Table 2. Lettuce consumption, egg mass, and egg production on each day of the feeding protocol. Data for MD (Medium Day) and LD (Long Day) animals. Means and standard deviations are given. There were three feeding schedules: 1, food every day; 2, food on days 1 and 2; 3, food on day 1 only. The data from the days the animals went without food are in italics.

Lettuce consumption (cm^2 per day per animal)

Day length	Food regimen	Day 1	Day 2	Day 3
MD	1	14.94 (3.27)	14.50 (3.45)	13.79 (3.39)
	2	23.71 (3.44)	17.86 (3.10)	*0.00 (0.00)*
	3	21.12 (4.09)	*0.00 (0.00)*	*0.00 (0.00)*
LD	1	16.35 (3.20)	16.14 (4.06)	16.09 (2.58)
	2	22.99 (5.18)	18.07 (5.02)	*0.00 (0.00)*
	3	14.47 (2.76)	*0.00 (0.00)*	*0.00 (0.00)*

Eggs per day per animal

Day length	Food regimen	Day 1	Day 2	Day 3
MD	1	13.62 (7.79)	15.39 (11.42)	16.31 (12.53)
	2	10.51 (9.35)	17.23 (12.31)	*4.33 (5.99)*
	3	1.53 (2.65)	*2.59 (3.86)*	*1.42 (3.17)*
LD	1	41.29 (27.14)	37.77 (17.61)	38.86 (18.50)
	2	36.79 (14.75)	27.05 (11.8)	*7.49 (6.85)*
	3	8.82 (6.53)	*15.16 (8.07)*	*15.50 (8.94)*

Egg masses per day per animal

Day length	Food regimen	Day 1	Day 2	Day 3
MD	1	0.15 (0.08)	0.17 (0.10)	0.18 (0.12)
	2	0.11 (0.09)	0.18 (0.11)	*0.04 (0.05)*
	3	0.02 (0.03)	*0.03 (0.04)*	*0.01 (0.03)*
LD	1	0.50 (0.22)	0.47 (0.14)	0.46 (0.21)
	2	0.59 (0.17)	0.49 (0.18)	*0.19 (0.13)*
	3	0.18 (0.15)	*0.27 (0.13)*	*0.30 (0.15)*

The relationship between egg production and consumption is shown (Fig 2). In groups 1 and 2, the slope of the fit was 2.247 and 2.211 eggs × cm^2 lettuce. In group 3, many animals did not lay eggs and there was no correlation between consumption and egg production. Combining all three groups yielded a slope of 1.419. In LD animals, all of which laid eggs, the slope of overall fit was 2.242 eggs per cm^2 lettuce. We conclude that an egg yield of about 2.2 eggs per cm^2 lettuce is a reasonable estimate.

Dry weight density in the field

Adults were present throughout the year and two generations partially overlap during the spring. Dry-weight densities were determined for 283 unparasitized specimens of *Lymnaea stagnalis* collected over the course of the year (Fig. 1). Dry-weight density varied during the year and was lower in summer, the season when most eggs are produced. The overall level of dry-weight density was lower in the field than in the laboratory. This was true for both long and short-day length conditions.

DISCUSSION

Food consumption

After starvation, individuals of *Lymnaea stagnalis* had higher consumption rates than snails that were fed continuously. Thus snails of group 2 appeared able to compensate for the day they were starved. This explains the relatively slight differences in growth and reproduction.

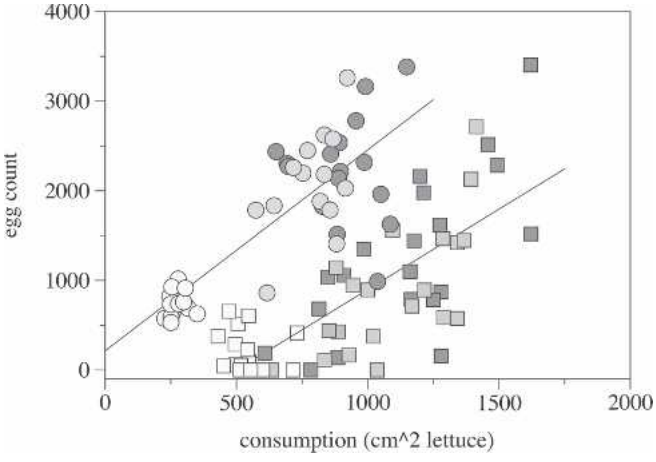

Figure 2. Relationship between food consumption and egg production in snails reared under LD (Long Day, circles) and MD (Medium Day, squares) conditions with the three feeding cycles. White fill, regimen 3; intermediate fill, regimen 2; dark fill, regimen 1. The lines are fitted to all the data of the MD and LD groups, respectively.

Growth

Bohlken and Joosse (1982) also studied the effects of day length on growth and reproduction in *Lymnaea stagnalis*. They reared a few hundred snails in one large tank under the same LD and MD conditions we used. We fitted growth curves to the data of Bohlken and Joosse (1982), yielding the following parameter estimates: for MD snails, $h_e = 3.54$ cm, $g = 0.014\ d^{-1}$; for LD snails, $h_e = 2.97$ cm, $g = 0.017\ d^{-1}$. The estimate for the growth rate parameter of MD snails corresponds to the one we determined for group 3 snails. The ultimate shell height for MD snails is equal to the one we found in the present experiment for the three groups; for LD snails it is between that of groups 2 and 3. This comparison suggests that in the experiment of Bohlken and Joosse (1982), food consumption was as limited as in our group 3. Data on the growth of snails that were kept individually and fed a limited amount of lettuce are provided by Geraerts (1976) and Bohlken *et al.* (1984). Growth curves were fitted to their data on control snails. In both cases, values of the growth rate parameter are in agreement with those found in the present study for the best-fed snails ($0.04 <$ growth rate < 0.06). Also, they were much higher than those reported by Bohlken and Joosse (1982). Apparently, snails kept in isolation have much better feeding conditions than do snails kept in large groups.

We found no differences between the ultimate shell heights of groups 1, 2, and 3 of MD snails. Thus the maintenance costs in these groups should eventually be identical. Because the rate of food intake was not identical, the less fed groups must allocate less energy to reproduction. Indeed, MD snails of group 2 produced fewer eggs than those of group 1, while the size differences between the snails were small throughout the experiment.

According to Kooijman (1993), the Von Bertalanffy growth coefficient decreases with increasing maximum storage capacity, because the animal has to build up the energy stores. The larger these stores, the longer it takes to build them up. LD snails had lower dry-weight densities than MD snails, so in all likelihood LD snails had less stored energy. In accordance with this prediction, LD snails had the higher Von Bertalanffy growth rates.

Input from the tentacles on the LGC, which produce a growth hormone related to insulin, may provide one way in which environmental factors could influence growth (Roubos and Van der Wal-Divendal 1982, Smit *et al.* 1988).

Timing of oviposition in relation to the food cycle

In both MD and LD snails, the timing of oviposition seemed to depend on the availability of food. However, MD

and LD snails reacted differently to the presence or absence of food. Both LD and MD snails suppressed egg laying when food was absent. Under LD conditions, egg-laying of group 2 was maximal on the first day after starvation. Under MD conditions, egg-laying in group 2 was maximal on the second day after starvation. A comparison with group 3 is not feasible because so few snails laid eggs. However, the fact that in LD snails in group 3 egg-laying was maximal on the second day of starvation is remarkable. Because snails of group 3 were starved for two days, the reduced egg laying on the day that the snails were fed might reflect a time-budget problem: the snails had no time to oviposit since they were busy feeding. However, this suggestion is not supported by the following observation. Snails of group 2 laid most egg masses on one of the days they were fed, whereas LD snails of group 3 laid most egg masses on one of the days they were starved. Yet the food-intake rates of groups 2 and 3 were equal. Hence we conclude that there was no time-budget conflict between egg-laying and feeding during the experiment.

A number of factors are known to affect the excitability of the egg-laying, hormone-producing CDC's, and hence egg laying. A discharge of this cell cluster is an all-or-nothing phenomenon; between discharges, the CDC remain electrically silent. One trigger for egg laying is a transfer from dirty to clean water (Clean Water Stimulus: Ter Maat *et al.* 1983). The present experiments suggest that food availability also affects the excitability of the CDC's, although indirectly, which is in agreement with electrophysiological findings (Ter Maat *et al.* 1982). Reduced food availability does not affect the size of the egg mass but does cause an increase of the interval between the deposition of successive egg masses. Before oviposition, energy allocated to reproduction is stored in various glands, including the albumen gland. The fact that both day length and food availability affect the reproductive rate but not the size of an egg mass suggests that oviposition is likely to occur if the gland's contents pass a certain threshold. This suggests that the filling of the albumen gland (and/or other glands) influences the excitability of the CDC's, possibly via the activation of stretch receptors. This idea is supported by the finding that in *Lymnaea stagnalis* albumen glands are heavier when the animals go longer without egg-laying (Koene and Ter Maat 2004). In contrast, in the garden snail *Helix aspersa* (Müller, 1774) the number of ripe oocytes in the ovotestis provides a permissive signal for the occurrence of egg-laying (Antkowiak and Chase 2003). We think that in *L. stagnalis*, storage of packaging material for the eggs is the critical factor in egg laying. Given these findings, it would be interesting to study whether egg-laying and the excitability of the CDCs depends on sensory signals from the albumen gland or from other accessory organs containing packaging material.

Comparison of MD and LD snails

Average somatic and reproductive production rate was a function of the average rate of food intake. Although such relationships are difficult to interpret, there was a clear difference between MD and LD snails. With regard to somatic production, however, there is no difference. There was a very clear difference in the reproductive output of MD and LD snails. At the same average food-intake rate, LD snails produced about 20 eggs per day more than MD snails. Qualitatively, this agrees with the observation that the daily egg production rate in LD snails was about 2 to 3 times that of MD snails.

If somatic production was more or less the same in LD and MD snails, how were LD snails able to maintain a much higher reproductive rate? LD snails had lower dry weights and therefore probably fewer energy reserves. The difference in dry weight acquired during the experiment for MD and LD snails, as calculated from the dry weight density and the volume increase, was about 0.12 g. The dry weight of eggs, including the capsule in which the eggs are embedded, is about 0.15 mg per egg (Zonneveld and Kooijman 1989). Hence the difference in acquired dry weight is equivalent to about 800 eggs. The experiment lasted for approximately 60 days, during which LD snails produced on the average 20 eggs per day more than did MD snails (1200 eggs more during the experiment). The difference in dry weight explains about 70% of this difference in egg production. Thus, we conclude that the difference in the rate of egg production was largely due to a decrease in energy reserves of LD snails compared to MD snails.

In the field, *Lymnaea stagnalis* is essentially an annual species, breeding in the summer season. Light conditions similar to our MD treatment are experienced in autumn and spring, during the juvenile period. It is advantageous to have large energy stores during this period, because food availability will be low and unpredictable. Light conditions similar to our LD treatment are experienced in the field in late spring and in the summer. Food availability will be predictably high in this period so there should be no need to have large energy stores. To maximize the reproductive output, the energy stores should be depleted. Our experiments were performed at a constant day length, while in the field, day length gradually increases to LD conditions with the onset of the summer. Hemminga *et al.* (1985) showed that snails indeed draw on their energy reserves after a change from a short to a long day length.

In conclusion, the current study shows that the high rate of reproduction under long day conditions can be maintained by keeping stores at a low level. In contrast, medium day animals invest more in storage, and lay eggs only when energy storage is above a certain level. The data on size and dry weight density in the field show a similar relationship

with day length as the laboratory data, in that long days are associated with high fecundity and low energy storage. However, a major difference between field and laboratory data is that dry weight densities are higher in the laboratory, presumably due to differences in feeding conditions.

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