Oecologia (1988) 77:390–394

Oecologia
© Springer-Verlag 1988

Population regulation in the land snail *Arianta arbustorum*: density effects on adult size, clutch size and incidence of egg cannibalism

B. Baur
Department of Zoology, Uppsala University, Box 561, S-751 22 Uppsala, Sweden

Summary. The relationships between local population density and adult size, clutch size and spatial distribution of egg batches were investigated in 11 natural populations of the land snail *Arianta arbustorum* in a forest near Uppsala, Sweden. Shell size of adults decreased with increasing population density as did clutch size. Within populations, clutch size scaled allometrically with shell size indicating size-specific fecundity. It is hypothesized that food unpalatability caused by mucus deposition slows down juvenile growth rate in high density populations, resulting in small adults and thus reducing their fecundity in subsequent years. The influence of the distance between batches on the incidence of egg cannibalism by hatchlings was examined in a laboratory experiment. In this experiment the number of eggs cannibalized increased with decreasing distance to the batch of hatching snails. Thus, in the field, eggs of highly aggregated batches suffer a high risk of cannibalism. In the 3 populations with the highest snail density, 21–39% of all batches were deposited close to each other (nearest neighbour distance ≤5 cm, i.e. less than hatchlings move within 1 day). These findings indicate that egg cannibalism can act as a population regulating factor.

Key words: Population regulation – Shell size – Fecundity – Cannibalism – Gastropoda

The potential for density-dependent regulation of population size by intraspecific interference has been long recognized (Nicholson and Bailey 1935; Solomon 1949; Chitty 1960). Various intraspecific mechanisms have been proposed for the control of density, such as dispersal (Wellington 1960), genetic feedback (Chitty 1960), stress (Christian and Davis 1964), territoriality (Rand 1967), social-dominance hierarchy (Watson and Moss 1970), habitat fouling (Barbosa and Peters 1970) and cannibalism (Fox 1975; Polis 1981).

Laboratory studies of terrestrial gastropods have shown that population density can have an important influence on juvenile growth rate, adult shell size and fecundity, even when excess food is available (Oosterhoff 1977; Cameron and Carter 1979; Dan and Bailey 1982; Reichardt et al. 1985). The effects have been ascribed to the density of mucus trails, which depresses the activity and hence food intake and growth rate of the snails (Oosterhoff 1977; Cameron and Carter 1979; Dan and Bailey 1982). As a result, snails grown up under crowded conditions have been found to attain a small adult size and to suffer a lowered fecundity.

In this paper I report on the relationships between local population density, adult shell size and clutch size in 11 natural populations of the land snail *Arianta arbustorum* (L.) in central Sweden. *A. arbustorum* hatchlings indulge in egg cannibalism, consuming still unhatched sibling eggs (= within-batch cannibalism) as well as eggs from neighbouring batches (= between-batch cannibalism) (Baur 1986a, 1987a, b; Baur and Baur 1986). While the degree of within-batch cannibalism in *A. arbustorum* depends exclusively on the extent of hatching asynchrony within egg batches (Baur and Baur 1986), the degree of between-batch cannibalism appears to depend on several factors, including the spatial distribution and density of egg batches, the hatching asynchrony between batches as well as the distances travelled by newly hatched snails (Baur 1987a, 1988a). To investigate the influence of the spatial distribution of egg batches on the extent of between-batch cannibalism, a laboratory experiment was performed. The results of this experiment and the dispersal distances of hatchlings measured in the field were related to the spatial distribution and density of egg batches found in the field. On the basis of these results the potential power of egg cannibalism as a density-regulating factor in natural populations of *A. arbustorum* will be evaluated.

Materials and methods

Relevant natural history

A. arbustorum is common in wet habitats in north-western and central Europe (Kerney and Cameron 1979). It is herbivorous and, like other helicids, hermaphroditic. Shell growth is restricted to spring and summer, and is completed after one or several hibernations with the formation of a shell lip at the edge of the shell aperture (Baur and Raboud 1988). In general, the formation of this lip indicates sexual maturity (but see Baur 1984a). The mean adult life span of *A. arbustorum* is 3–4 years, but a maximum longevity of 14 years after reaching sexual maturity has been recorded (Raboud 1986; Baur and Raboud 1988). *A. arbustorum* lays its eggs in batches (1–3 clutches per year) in small holes in the soil or among decaying grass or moss (Baur 1988a; Baur and Raboud 1988). The eggs are 2.7–3.2 mm in diameter, depending on the mother's size (Frömming 1954; Baur 1984b). Emerging snails first eat their own egg shell and

---

* *Present address and address for offprint requests:* Zoology Institute, University of Basel, Rheinsprung 9, CH-4051 Basel, Switzerland

then consume unhatched eggs, including ones with fully developed embryos (Baur and Baur 1986). This type of egg predation only occurs during the hatchling stage (Baur 1987b), and only conspecific eggs are eaten (Baur 1988b). Cannibalistic hatchlings are unable to discriminate between kin and non-kin eggs (Baur 1987a).

Study site and general methods

Field work was conducted in clearings and local stands of ash (*Fraxinus excelsior*) and aspen (*Populus tremula*) in the pine (*Pinus silvestris*) dominated forest Stadsskogen near Uppsala, central Sweden (59°50′N, 17°40′E). *A. arbustorum* is abundant in both habitats. The clearings, 0.01–0.4 ha in size, were coverd by *Cirsium arvense* and various species of grass.

The density of adult *A. arbustorum* was estimated by using a mark-recapture procedure at 11 distinct sites. These sites – for convenience hereafter referred to as populations – were all situated within an area of 0.5 km^2, but at least 30 m apart from each other and mostly separated by coniferous woodland. At each site the vegetation and leaf litter (including the upper layer of soil) were carefully searched for adults and egg batches of *A. arbustorum* by sampling 8–64 adjacent quadrats of 0.5 m^2 in August 1987 (=peak of egg-batch occurrence). Size of adult snails (diameter and height of the shell) was measured to the nearest 0.1 mm using a vernier caliper and shell volume was calculated according to the formula given by Rensch (1932):

$$\text{Shell volume} = (\text{diameter})^2 \times \text{height}/2.$$

In each population on average 37 snails (range 20–53) were measured. Each snail was marked with a dot of nail varnish and immediately released at the place where it was found. The positions of all egg batches within each quadrat were mapped. In four populations the number of eggs of each batch were counted. Recapture of snails occurred one day after release and population density was estimated using the Lincoln index (Begon 1979). The efficiency of the sampling method was tested by repeating the procedure in four quadrats, removing the vegetation and upper layer of soil. This improved method demonstrated that the normal sampling procedure revealed more than 90% of the egg batches and 45–65% of adult snails.

To assess the relationship between shell size and clutch size snails from a population 3 km away from Stadsskogen were kept singly in boxes for 20 days. To offer appropriate egg-laying sites the bottom of each box was provided with two pits, which were filled with soil. Caged snails were fed fresh lettuce ad libitum and 77 out of 113 individuals deposited one clutch within 20 days.

To estimate dispersal distances of *A. arbustorum* hatchlings in the field, 60 newly hatched snails (1-day-old) were marked with a minute dot of correction fluid ('Tipp-Ex') and released at two sites in Stadsskogen. Their displacements were subsequently recorded after 1, 2 and 3 days, respectively. During this experiment the vegetation near the ground was slightly moist, but no rain fell.

Laboratory experiment

A laboratory experiment was designed to investigate the influence of the spatial distribution of egg batches on the extent of between-batch cannibalism. For simplicity, the number of egg batches was kept at two, clutch size was constant and hatching asynchrony between batches was assumed to exceed 5 days, while the distance between the two batches was varied. For this purpose 30 newly hatched snails (2-day-old and younger) were placed very close to each other (simulating emerging snails) in a container (24.7 × 18 × 7 cm) 0, 2.5, 5, 7.5, 10, 15 or 20 cm apart from a batch of 30 eggs. The bottom of the container was covered with moist soil and 4 leaves of lettuce were placed on top of it. Containers were kept at 20–22° C and under natural light conditions. Experiments were run for 3 days, after which the number of eggs consumed was recorded. A total of 24 trials were run; each hatchling was tested only once. For each trial the containers were washed and soil, lettuce and eggs replaced.

I used linear regression of $\log_{10}$-transformed values (which at first were $X+1$ and $Y+1$ transformed because zero values occurred) to analyse the relationship of the distance between hatchlings and eggs and the number of eggs cannibalized.

Results

Local population density, adult size and clutch size

The local population density of *A. arbustorum* ranged from 1.9 to 10.8 adults per m^2, but no relationship between snail density and habitat type (clearing or woodland) could be found (Table 1). The pattern of population density was similar to that in 1986 (B. Baur, unpublished work).

Adult size of *A. arbustorum* decreased with increasing local population density (Fig. 1). Measurements of adult shell diameter showed a decrease of 1.5 mm (6.9%) associated with an increase in density from 1.9 to 10.5 adults per m^2. Adult shell volume decreased by 18.6% within the same range of population density.

Clutch size was negatively correlated with local population density ($r=-0.971$, $N=4$, $P=0.029$) (Table 1). Furthermore, clutch size scaled allometrically with shell size in snails kept singly in boxes during egg-laying (Fig. 2). For an increase in shell diameter of 1 mm clutch size increased by 6.2 eggs

The density of egg batches in the field ranged from 0.2 to 21.0 per m^2 and was positively correlated with local population density ($r=0.689$, $N=11$, $P=0.019$) (Table 1). The mean distance to the nearest neighbour batch ranged from 10.5 to 160 cm (Table 1). In populations with very high batch density (populations 1–3 in Table 1), 21–39% of all batches were deposited 5 cm or less away from their nearest neighbour batch and 43–58% within 10 cm. Both the proportion of egg batches deposited within a nearest neighbour distance (D) of 5 and 10 cm, respectively, were positively correlated with local population density (for $D=$ 5 cm: $r=0.677$, $N=11$, $P=0.021$; for $D=10$ cm: $r=0.726$, $N=11$, $P=0.011$) (Table 1).

Dispersal of hatchlings in the field

Displacements of newly hatched *A. arbustorum* after 1 day averaged 5.8 cm (range: 2–12 cm, $N=9$). The corresponding figures after 2 days were 8.0 cm (range 3–20 cm, $N=5$) and after 3 days 13.8 cm (range: 8–25 cm, $N=4$). The proportion of recaptured hatchlings was low; decreasing from 15.0% after 1 day to 6.7% after 3 days.

Table 1. Density of snails and egg batches, clutch size and characteristics of egg-batch dispersion in 11 populations of *A. arbustorum*

Population	No. of adult snails per m² $\bar{x}\pm$SE	No. of egg batches per m² $\bar{x}\pm$SE	Clutch size $\bar{x}\pm$SE	Distance to nearest neighbour batch $\bar{x}$ (*N*)	Proportion of egg batches deposited within a nearest neighbour distance of	
					≤5 cm	≤10 cm
Grassland (clearings)						
1	10.5±0.8	21.0±0.5	27.6±1.9	11.0 (110)	0.29	0.45
2	6.6±1.1	15.5±0.4	34.0±3.3	10.5 (31)	0.39	0.58
3	10.8±1.3	7.8±0.7	–	14.2 (47)	0.21	0.43
4	7.3±1.2	5.2±0.5	–	21.7 (26)	0	0.15
5	5.5±1.6	4.3±0.4	–	24.5 (17)	0	0
6	6.5±1.4	3.5±0.9	36.0±4.1	21.4 (21)	0.10	0.29
7	5.7±1.4	3.0±0.5	35.5±7.0	24.2 (18)	0.11	0.17
8	5.7±1.1	3.0±0.6	–	25.1 (18)	0	0.11
9	4.3±0.6	2.3±0.6	–	27.8 (14)	0	0
Woodland						
10	6.3±1.0	3.3±0.3	–	30.0 (27)	0.07	0.15
11	1.9±0.5	0.2±0.2	–	160.0 (3)	0	0

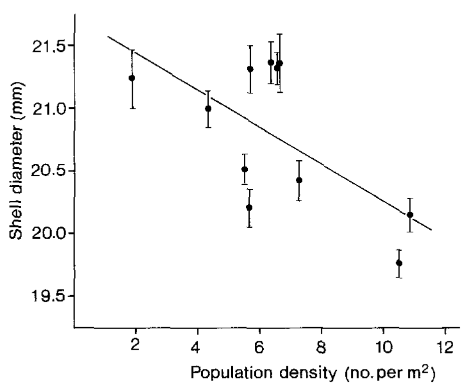

Fig. 1. Relationship between mean adult shell diameter (±SE) and adult population density in *A. arbustorum*. $Y=21.73-0.146X$, $N=11$, $r^2=0.396$, $P=0.038$ (standard error of slope $=0.060$)

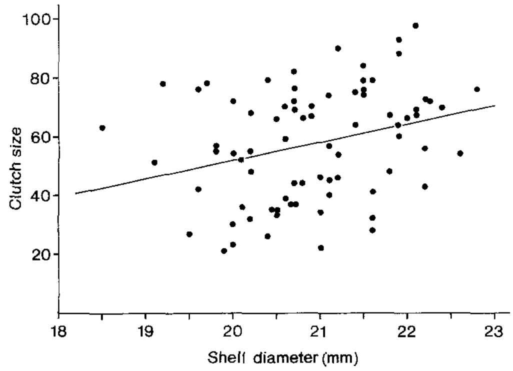

Fig. 2. Relationship between clutch size and shell diameter in *A. arbustorum*. Snails were kept singly in boxes for oviposition. $Y=6.21X-72.20$, $N=77$, $r^2=0.086$, $P=0.0095$ (standard error of slope $=2.33$)

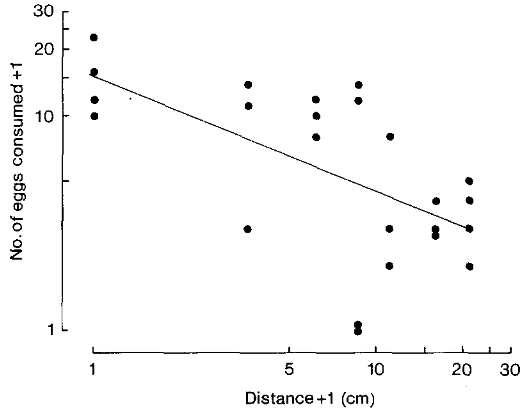

Fig. 3. The number of eggs cannibalized (+1) within 3 days by 30 newly hatched *A. arbustorum* as a function of the distance (+1) between their place of release ('hatching') and a batch of 30 unhatched eggs. $\mathrm{Log}_{10}(Y+1)=1.18-0.53\log_{10}(X+1)$, $N=24$, $r^2=0.378$, $P=0.0014$

Egg cannibalism in the laboratory experiment

The number of eggs consumed by hatchlings decreased with increasing distance between their place of release and the batch with unhatched eggs (Fig. 3). Thirty *A. arbustorum* consumed on average 14.3 eggs (47.5%) within 3 days when they were released side by side of a batch consisting of 30 unhatched eggs (Fig. 3). The corresponding figures were 9.0 eggs (30.0%) for a distance of 5 cm between 'hatching' snails and the unhatched eggs, 3.3 eggs (11.1%) for 10 cm and 2.5 eggs (8.3%) for 20 cm.

Discussion

The present study demonstrates a decrease in adult shell size with increasing density of *A. arbustorum* in the field. A similar density-dependent decrease of adult shell size was found in natural populations of the land snails *Cepaea nemoralis, Helicella itala, Candidula intersecta* and *Cochlicella acuta* (Williamson et al. 1976; Tattersfield 1981), as well as in several other species in laboratory studies (see review in Goodfriend 1986). The range of adult density found in Stadsskogen does not exceed those reported in other studies on *A. arbustorum* (0.6–17.3 adults per m²; see review in Baur 1986b).

Juvenile *A. arbustorum* showed a reduced growth rate when reared under conditions of high density in the laboratory, even if waste products were removed (Reichardt et al. 1985). Moreover, it has been shown in *C. nemoralis* and *H. aspersa* that the smaller adult size attained at higher densities is caused by a lower growth rate (Oosterhoff 1977; Cameron and Carter 1979; Lucarz 1982). The lower growth rate is apparently a result of inhibition of activity at high densities. This inhibition has been shown experimentally to be proximately caused by an unidentified pheromone present in snail mucus (Cameron and Carter 1979; Dan and Bailey 1982).

The present study demonstrates a positive relationship between adult shell size and clutch size. In other populations of *A. arbustorum* I have previously found that the total number of eggs produced per year and egg size scaled allometrically with adult shell size (Baur 1984b; Baur and Raboud 1988). Thus, one can safely assume that bigger snails have a higher reproductive output than smaller ones. However, the size-related reproductive characters varied considerably among populations, most probably indicating interactions of size with genetic factors. In addition to the size-specific fecundity, a direct influence of density on clutch size, hatching success and mortality has been demonstrated experimentally in *A. arbustorum* (Reichardt et al. 1985; for other species see Wolda 1970; Yom-Tov 1972; Oosterhoff 1977). Hence, the population density of *A. arbustorum* appears to be regulated via growth rate, adult shell size and fecundity. Growth rate is reduced due to habitat fouling by an increasing density of mucus trails of conspecifics rather than by food shortage. In fact, there was no trace of any food shortage in the populations investigated, but *Cirsium arvense* (a food plant preferred by *A. arbustorum* (Frömming 1954; B. Baur, unpublished work)) was often seen to be completely covered by mucus trails in areas with high snail densities. Intraspecific interference by mucus deposition therefore may be a major factor for density-regulation in *A. arbustorum.*

Dispersal often increases in high density populations (Swingland and Greenwood 1983). In *C. nemoralis* dispersal was found to be inversely related to population density (Cain and Currey 1968; Greenwood 1974; Oosterhoff 1977), and Oosterhoff (1977) stated that dispersal is an important factor for the regulation of population size in this species. Similar information for *A. arbustorum* is not available.

Cannibalism as a factor regulating local population size has recently received increasing attention in numerous animal species (e.g. Polis 1980; 1981; Harris 1987). *A. arbustorum* prefers to lay its eggs at places with high moisture content (Baur 1988a). When starting to oviposit a snail does not react to the presence of conspecific eggs, thus exposing its eggs to the risk of between-batch cannibalism (Baur 1988a). As a result of the spatial heterogeneity of habitats, egg batches can be found in a highly aggregated pattern, above all in habitats with high population density (Baur 1988a). In the laboratory, the extent of egg cannibalism increased with decreasing distance between egg batches. In the field, habitat structure may be more complex than in my laboratory experiment, and consequently fewer hatchlings will move from their place of emergence to a neighbour batch. On the other hand, one egg batch is often surrounded by several other egg batches, and furthermore land snails are known to locate food by chemical cues (Croll 1983). Between-batch cannibalism could actually be observed in populations of *A. arbustorum* in Stadsskogen (Baur 1987a). My experiment and the dispersion of egg batches found in the field indicate that between-batch cannibalism may occur above all in high density populations. Thus, egg cannibalism can act as a regulating factor in *A. arbustorum.*

Apart from self-regulation, predation by birds (family Turdidae), toads, shrews, ground beetles and snails as well as parasitism may influence population density in *A. arbustorum* (for lists of potential predators see Wild and Lawson 1937; Reichardt et al. 1985). The influence of predators and parasites may vary between different populations. In Stadsskogen I frequently observed the zonitid snail *Oxychilus alliarius* preying upon eggs and juveniles of *A. arbustorum.* Furthermore, 27 out 36 egg batches (1004 eggs) collected in population 1 (see Table 1) were parasitized by dipteran larvae (family Phoridae), resulting in an average hatching success of 32.2% (range 0–97.6%) (B. Baur, unpublished work). However, quantitative estimates of the total impact of predators and parasites on land snail populations have never been published.

In addition, of course, abiotic factors such as drought or extreme cold prior to the formation of a snow cover or following snowmelt can cause high mortality in snail populations (cf. Stöver 1973; Terhivuo 1978). For example, Williamson (1958) suggested that a shortage of suitable shelter sites can regulate the density of snail populations.

In conclusion, population size of *A. arbustorum* may be controlled by a complex of factors varying in space and time. Adult shell size and fecundity were found to decrease with increasing population density indicating that habitat fouling due to mucus trails acts as a regulating mechanism. In addition, egg cannibalism by hatchlings may contribute to a reduction of population fluctuations.

Acknowledgements. I thank M. Malmquist, A.P. Møller and S. Ulfstrand for constructive criticism on the manuscript. Financial support was received from the Swiss National Science Foundation.

References

Barbosa P, Peters TM (1970) The manifestations of overcrowding. Bull Entomol Soc Am 16:89–92

Baur B (1984a) Early maturity and breeding in *Arianta arbustorum* (L.) (Pulmonata: Helicidae). J Moll Stud 50:241–242

Baur B (1984b) Shell size and growth rate differences for alpine populations of *Arianta arbustorum* (L.) (Pulmonata: Helicidae). Rev Suisse Zool 91:37–46

Baur B (1986a) The influence of cannibalistic egg eating on the growth of young *Arianta arbustorum* (L.) (Helicidae). Snail Farming Res 1:9–17

Baur B (1986b) Patterns of dispersion, density and dispersal in alpine populations of the land snail *Arianta arbustorum* (L.) (Helicidae). Holarct Ecol 9:117–125

Baur B (1987a) Can cannibalistic hatchlings of the land snail *Arianta arbustorum* distinguish between sib and non-sib eggs? Behaviour 103:259–265

Baur B (1987b) Effects of early feeding experience and age on the cannibalistic propensity of the land snail *Arianta arbustorum.* Can J Zool 65:3068–3070

Baur B (1988a) Do the risks of egg cannibalism and desiccation influence the choice of oviposition sites in the land snail *Arianta arbustorum*? J Zool (in press)

Baur B (1988b) Egg-species recognition in cannibalistic hatchlings of the land snails *Arianta arbustorum* and *Helix pomatia.* Experientia 44:276–277

Baur B, Baur A (1986) Proximate factors influencing egg cannibalism in the land snail *Arianta arbustorum* (Pulmonata, Helicidae). Oecologia (Berlin) 70:283–287

Baur B, Raboud C (1988) Life history of the land snail *Arianta arbustorum* along an altidudinal gradient. J Anim Ecol 57:71–87

Begon M (1979) Investigating animal abundance. Edward Arnold, London

Cain AJ, Currey JD (1968) Studies on *Cepaea*. III. Ecogenetics of a population of *Cepaea nemoralis* (L.) subject to strong area effects. Philos Trans R Soc London Ser B 253:447–482

Cameron RAD, Carter MA (1979) Intra- and interspecific effects of population density on growth and activity in some helicid land snails (Gastropoda: Pulmonata). J Anim Ecol 48:237–246

Chitty D (1960) Population processes in the vole and their relevance to general theory. Can J Zool 38:99–113

Christian JJ, Davis DE (1964) Endocrine, behavior and population. Science 146:1550–1560

Croll RP (1983) Gastropod chemoreception. Biol Rev 58:293–319

Dan N, Bailey SER (1982) Growth, mortality, and feeding rates of the snail *Helix aspersa* at different population densities in the laboratory, and the depression of activity of helicid snails by other individuals, or their mucus. J Moll Stud 48:257–265

Fox LR (1975) Cannibalism in natural populations. Annu Rev Ecol Syst 6:87–106

Frömming E (1954) Biologie der mitteleuropäischen Landgastropoden. Duncker and Humblot, Berlin

Goodfriend GA (1986) Variation in land-snail form and size and its causes: a review. Syst Zool 35:204–223

Greenwood JJD (1974) Effective population numbers in the snail *Cepaea nemoralis*. Evolution 28:513–526

Harris RN (1987) An experimental study of population regulation in the salamander, *Notophthalmus viridescens dorsalis* (Urodela: Salamandridae). Oecologia (Berlin) 71:280–285

Kerney MP, Cameron RAD (1979) A field guide to the land snails of Britain and north-west Europe. Collins, London

Lucarz A (1982) Effect du groupement sur la croissance pondérale d'escargots *Helix aspersa* Muller. C R Acad Sci 294:753–756

Nicholson AJ, Bailey VA (1935) The balance of animal populations. Proc Zool Soc London [Part I, 1935]:551–598

Oosterhoff LM (1977) Variation in growth rate as an ecological factor in the landsnail *Cepaea nemoralis* (L.). Neth J Zool 27:1–132

Polis GA (1980) The effect of cannibalism on the demography and activity of a natural population of desert scorpions. Behav Ecol Sociobiol 7:25–35

Polis GA (1981) The evolution and dynamics of intraspecific predation. Annu Rev Ecol Syst 12:225–251

Raboud C (1986) Demographische Altersverteilung bei *Arianta arbustorum* (L.) (Mollusca, Pulmonata) in Abhängigkeit von der Höhe über Meer. PhD Thesis, Univ of Zurich

Rand AS (1967) The adaptive significance of territoriality in iguanid lizards. In: Milstead WW (ed) Lizard ecology: a symposium. University of Missouri Press, Columbia, MO

Reichardt A, Raboud C, Burla H, Baur B (1985) Causes of death and possible regulatory processes in *Arianta arbustorum* (L., 1758) (Pulmonata, Helicidae). Basteria 49:37–46

Rensch B (1932) Über die Abhängigkeit der Größe, des relativen Gewichtes und der Oberflächenstruktur der Landschneckenschalen von den Umweltsfaktoren. Z Morphol Ökol Tiere 25:757–807

Solomon ME (1949) The natural control of animal populations. J Anim Ecol 18:1–35

Stöver H (1973) Cold resistance and freezing in *Arianta arbustorum* (L.) (Pulmonata). In: Wieser W (ed) The effects of temperature on ectothermic organisms. Springer, Berlin Heidelberg New York

Swingland IR, Greenwood PJ (1983) The ecology of animal movement. Clarendon Press, Oxford

Tattersfield P (1981) Density and environmental effects on shell size in some sand dune snail populations. Biol J Linn Soc 16:71–81

Terhivuo J (1978) Growth, reproduction, and hibernation of *Arianta arbustorum* (L.) (Gastropoda, Helicidae) in southern Finland. Ann Zool Fenn 15:8–16

Watson A, Moss R (1970) Dominance, spacing behaviour and aggression in relation to population regulation in vertebrates. In: Watson A (ed) Animal populations in relation to their food resources. Blackwell Scientific, London

Wellington WG (1960) Qualitative changes in natural populations during changes in abundance. Can J Zool 38:289–314

Wild SV, Lawson AK (1937) Enemies of the land and freshwater Mollusca of the British isles. J Conchol 20:351–361

Williamson MH (1958) An apparently simple case of population control. Nature 182:1008

Williamson P, Cameron RAD, Carter MA (1976) Population density affecting adult shell size of snail *Cepaea nemoralis* L. Nature 263:496–497

Wolda H (1970) Variation in growth rate in the landsnail *Cepaea nemoralis*. Res Popul Ecol (Kyoto) 12:185–204

Yom-Tov Y (1972) Field experiments on the effect of population density and slope direction on the reproduction of the desert snail *Trochoidea (Xerocrassa) seetzeni*. J Anim Ecol 41:17–22

Received: Mai 12, 1988