

**Causes of death and possible regulatory processes
in *Arianta arbustorum* (L., 1758) (Pulmonata, Helicidae)**

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CONTENTS

1. Introduction	37
2. Abiotic agents	37
3. Predation by birds	38
4. Predation by mammals	39
5. Predation by invertebrates	40
6. Parasitism	40
7. Competition for food	40
8. Self-regulation	41
9. Discussion	44
10. Summary	44
11. References	44

1. INTRODUCTION

In the eastern part of the Swiss midlands as well as various alpine regions, we have found *Arianta arbustorum* (L., 1758) in countless places, provided the soil contained calcium. Habitats include borders of brooks, deciduous forests, hedges, verges of roads, marshes and alpine grassland. In many places where the species occurs it is abundant. In some places it is superabundant, density reaching or surpassing 100 snails per m². The pattern of dispersion seems to be rather stable, since where *A. arbustorum* was abundant in 1975 when we began to collect systematically, it was abundant thereafter on every check, and where it was absent in 1975, it has never been found since. We do not know by what processes the abundance at each place is maintained. In the following, we report on causes of death which might contribute to regulation, and give evidence of a tendency towards self-regulation.

Since *A. arbustorum* is highly variable in phenotype (Burla & Stahel 1983, for reference) selective mortality might alter the frequency of morphs. This possibility is kept in mind while presenting the observations. While some of our observations were made accidentally, others are the results of short studies.

2. ABIOTIC AGENTS

A. arbustorum has the perilous habit of dwelling near bodies of water, and of crawling into temporarily dry brooks. With rain, such snails are carried away and may be drowned.

In the Alps, another danger comes from avalanches. In the course an avalanche takes, the soil is eroded and displaced together with hibernating snails. In avalanches

that had come to rest, we found *A. arbustorum* of which a proportion had survived. The chance of survivors to reach feeding grounds may be small, and the period left for their reproduction may become short.

At several alpine sites we have seen numerous dead *A. arbustorum* early in spring. Of the retracted body, just a motionless tip of the foot was showing, as has been described by Richardson (1974) for *Cepaea nemoralis* (L., 1758). We imagine that the snails had been driven out of their hides by water from melting snow, whereupon the snails were exposed to deadly insolation. Later in the year, living *A. arbustorum* could be seen again at the same places. We imagine that gullies are particularly dangerous, whereas ridges are areas of refuge from where the gullies are re-colonized. While abiotic agents generally are not accepted as a means of regulation, the presence of refuges is. They help to maintain a constant number of survivors (Murdoch & Oaten, 1975). Williamson (1958) has suggested that a shortage of suitable hibernating sites may limit the population size of *Helix aspersa* Müller, 1774.

During a period of high temperatures and drought (July 1983), dead *A. arbustorum* could be seen by the hundreds on grassland in the area of Savognin, from 1200 to 2000 m above sea level. From their abundance, we guess that a considerable fraction of the population had succumbed to heat and drought. Prolonged drought and high temperatures are known to be harmful for the species (Grainger, 1969) and other snails. In *Achatina fulica* Bowdich, 1822, and *Macrochlamys indica* (Pfeiffer, 1846) the mortality rate is higher in the aestivating period than during activity (Raut & Ghose, 1981). In *C. nemoralis* the oviposition frequency decreases during long periods of drought (Wolda, 1965).

3. PREDATION BY BIRDS

In some forests of the Swiss midlands we confirmed the findings that blackbirds (*Turdus merula*) (Di Cesnola, 1907; Eble, 1963) and song thrushes (*Turdus philomelos*) (Parkin, 1971, 1973; Reichholf, 1979) prey on *A. arbustorum*. Song thrushes pick up snails from the ground and open the shell on an anvil. This is true for *A. arbustorum* (Cameron, 1969; Parkin, 1971; Reichholf, 1979) in the same way as for *C. nemoralis* (Cain & Currey, 1968; Cameron, 1969; Richardson, 1975). Most snails thus caught are opened at the apex and the spindle is broken, while the orifice remains intact (Morris, 1954). On the Col de Balme near Martigny at 2200 m mistle thrush (*Turdus viscivorus*) and ring ouzel (*Turdus torquatus*) opened shells of *Cepaea* and *Arianta* in the same manner (personal communication by Dr. F. Catzeflis, Lausanne). On a subalpine meadow, Potersalp near Appenzell at 1300 m, thrush anvils with broken shells of *A. arbustorum* were numerous. In a dry brook in a coniferous forest above Savognin at 2000 m we collected the remains of approximately 100 *A. arbustorum* shells that probably had been opened by mistle thrushes. Of 121 droppings of alpine choughs (*Pyrrhocorax graculus*) collected in an alpine meadow at 2500 m above Davos, 63 contained pieces of *A. arbustorum* shells. In the castle of Riom near Savognin, at 1300 m, where a large colony of jackdaws (*Corvus monedula*) breeds regularly, 12 droppings out of 200 contained remains of *A. arbustorum* shells. On 14 March 1976, 17 lapwings (*Vanellus vanellus*) had been observed to skim the meadow at Salouf in the vicinity of Savognin. Inspection of the place showed intact *A. arbustorum*, in abundance, along with broken shells. Very likely the species falls prey to more bird species than mentioned by us. By their size and soft shell, juvenile *A. arbustorum* are exposed even to small species of carnivorous birds (Eble, 1963).

In our midland study areas, the observations of predation of *A. arbustorum* by thrushes were made in summer, whereas the droppings of alpine choughs above Davos had been collected at a time when, in late spring, the melting snow exposed *A. arbustorum* habitats on which the choughs foraged. Local conditions and season will influence the toll that the snail pays to its predators. In *Cepaea* predation by birds was observed to take place both in summer (Cain & Currey, 1968; Williamson et al., 1977) and in winter (Richardson, 1975).

The time when birds can meet *A. arbustorum* is limited to the overlap in activity periods of prey and predator, the birds mentioned being diurnal whereas the snail is mostly nocturnal. During the middle of the day most *A. arbustorum* are hidden, many being burrowed in the soil. The time of activity overlap is wide in the case of thrushes, which forage from dawn to dusk, while it is limited in alpine choughs which forage from late morning to early evening. Moreover, alpine choughs forage on traditional areas that are many times larger than the area of a local population of *A. arbustorum*. If such birds move around restlessly, they do not find time to deplete a local snail population. They skim the surplus of snails rather than drive them to extinction.

Since the birds mentioned locate their prey visually, different colour morphs of *A. arbustorum* probably are not perceived at the rate of their occurrence. In deciduous forests, at anvils of song thrushes, broken pale shells are found at a frequency exceeding that of pale snails in the population (Parkin, 1971; Reichhoff, 1979). On alpine grassland, the shell colouring of *A. arbustorum* tends to be monomorphously pale, so that visual selection does not apply. The question remains whether monomorphism here is a result of previous predation.

4. PREDATION BY MAMMALS

Unlike thrushes, small mammals cut holes with jagged outlines into the shell, often beginning at the orifice (Morris, 1954). We are, however, unable to tell from cuts which mammal species was at work.

We offered *A. arbustorum* to captive small mammals: two hedgehogs (*Erinaceus europaeus*), a common shrew (*Sorex coronatus*), three longtailed fieldmice (*Apodemus sylvaticus*), two bank voles (*Clethrionomys glareolus*), a field vole (*Microtus agrestis*) and a squirrel (*Sciurus vulgaris*). The hedgehogs were proficient in eating *A. arbustorum*, young and adult, and left no debris of shells. The common shrew accepted young snails up to 10 mm diameter in large numbers. The longtailed fieldmice did the same, but refused adult snails, which the shrew handled, though inefficiently. The bank voles ignored the snails, as did the field vole. The squirrel tossed the snails around without eating them.

Where rats are present, they may limit snail populations. In a population of *H. aspersa*, Potts (1975) attributed 74% of the mortality to predation by black rats (*Rattus rattus*). Small mammals mostly forage at night. If they contribute to the regulation of snail density, they probably do it irrespective of prey colour. Only the longtailed fieldmouse is active in the daytime and therefore might be capable of visual hunting and selective predation.

We offered *A. arbustorum* furthermore to five cows and three captive red deer (*Cervus elaphus*). For this purpose the snails were inserted in portions of green food plants. The deer tested the snails with their lips and tongues and spat them out. The cattle did the same when the lips touched the shell, but chewed those snails that passed the lips unnoticed. Wild ungulates as well as cattle on pasture graze from dusk to dawn and

thereby come across *A. arbustorum*, which has the same schedule of activity. It is unlikely that these ungulates limit *A. arbustorum* populations, either by eating or trampling them.

5. PREDATION BY INVERTEBRATES

We have also offered *A. arbustorum* to invertebrates. Larvae of the beetles *Carabus auronitens* and *Drilus spec.* fed on adult snails. Various small carabid beetles, e.g., *Anisodactylus binotatus*, feed on juvenile *A. arbustorum*. A larva of *Lampyris noctiluca* selected juvenile snails of between 5 and 9 mm width for eating, and killed an adult *A. arbustorum* when no other food was offered. A starving chilopod, *Lithobius forficatus*, accepted freshly hatched *A. arbustorum*. These observations are very limited. There must be many more invertebrates which feed on *A. arbustorum* or their eggs, either occasionally or regularly.

Predators of *Helix pomatia* L., 1758, are *Carabus violaceus*, *Feronia melanaria*, *F. madida*, *Lampyris noctiluca*, and *Ocypus olens* (see Pollard, 1975). Wolda (1963) and Cain & Currey (1968) observed the snail *Oxychilus cellarius* (Müller, 1774) eating eggs of *C. nemoralis*.

6. PARASITISM

At three alpine sites, many lifeless *A. arbustorum* were seen in June 1981. Of 115 such snails not one did recover, but 14 dipteran larvae (Syrphidae and Tachinidae) emerged from them. We assume that the snails had been infested with fly eggs after death or while in a moribund state. From the same three sites 67 living *A. arbustorum* were caged under regular conditions of care. Within two months 29 died, which is an unusually high death rate. Since no macroscopic parasite emerged, the cause of death remained unknown. To collect more data, 300 adult *A. arbustorum* from a wood near Zurich were taken into captivity in the laboratory for one month. During this period only one snail died and no parasites were found.

In Norway, *A. arbustorum* is susceptible to infection by the nematode *Elaphostrongylus rangiferi*, which uses terrestrial gastropods as intermediate hosts (Skorping & Halvorsen, 1980).

7. COMPETITION FOR FOOD

A. arbustorum has been observed to consume plants of many species in the wild (Lindquist, 1941; Frömning, 1954; Grime & Blythe, 1969) and still more in captivity (Frömning, 1937; Mason, 1970). Even if it seems to have preferences (nettles, thistles, dog's mercury) *A. arbustorum* as a food generalist can switch from one plant to another according to the supply. In *C. nemoralis* the diet changed according to the availability of preferred materials during the year (Williamson & Cameron, 1976). Mason (1970) reported that *A. arbustorum* was largely feeding on dead plant material and that it took only a small proportion of living material. It also ate fungi and soil and may be saprophagous. Should it be able to digest micro-organisms, its vast area of occurrence and wide ecological niche would be understandable.

Even in places where *A. arbustorum* is superabundant, no depletion of plant biomass was noticed. However, food limitation is hard to assess without accurate knowledge of the consumer's vital requirements. One should also know how well *A. arbustorum*

assimilates each plant species that it devours. Where food appears to be ample, crowding of snails may, all the same, reduce their growth and hence their fecundity, as Tattersfield (1981) has discussed for three helioid species. There may be critical levels for certain components of the diet, below which the remainder cannot be properly utilized. Wolda et al. (1971) pointed out that more than one energy source is required, and it may be that trace elements or other compounds limit the number of snails. Grime et al. (1970) have suggested that a shortage of phosphorus was limiting the number of *C. nemoralis*. Nothing is known of the nutritional requirements of *A. arbustorum*, but studies by Howes & Whellock (1937) on the growth of *H. pomatia* showed that this species needed vitamins A and B and some sterols. Wagge (1952) found that adult *Helix* require sitosterol. In spite of being a food generalist, *A. arbustorum* may be limited in presence and abundance by the quality of its food in the way that was reported for *Helicella virgata* (Da Costa, 1778) by Butler (1976).

At places where *A. arbustorum* is easily found, it appears to be the dominant species of the respective snail communities, and we guess that there it suffers little competition from other snail species that might share its diet. Up to about 1800 m of altitude *Bradybaena fruticum* (Müller, 1774) is seen along with *A. arbustorum*, though in smaller numbers, and the same applies to *Helix pomatia* up to 2000 m. The much smaller *Trichia villosa* (Studer, 1789) is frequently seen in the same places where *A. arbustorum* hides. It cannot be excluded that *A. arbustorum* experiences subtle interspecific competition, as has been shown to exist between *C. nemoralis* and *C. hortensis* by Carter et al. (1979).

8. SELF-REGULATION

In captive *Lymnaea stagnalis* (L., 1758), reproduction is low when population density is high (Mooij-Vogelaar et al., 1970). We adopted the same scheme to test *A. arbustorum* for self-regulation. Virgin snails were confined in plastic boxes, 18.5 x 8.5 x 13 cm in size, at densities of 2, 4 and 8 snails per box, each density in five replicates. The snails were fed according to demand, and the eggs they laid were counted for 14 weeks. From 2 to 8 parents, litter size declined (fig. 1). The number of young snails reared from each clutch declined even more strongly with increasing parent density, indicating an effect of parent density on hatching success (fig. 2).

The same experimental design was used again to check for the influence of density on the later performance of offspring. Ten-day-old siblings were allowed to develop with 2, 4, 8 and 16 per cage, in four replicates each. Growth rate decreased with density (fig. 3) and death rate increased with density (fig. 4).

All effects, though small, point toward self-regulation. Yet at least part of the effects might be caused by confinement. By moving around, caged snails spoil the food with mucus. Mucus also covers the walls of the container and the soil on the bottom. Through this, living conditions deteriorate the more snails there are in a box. This effect would be less drastic in a highly structured natural environment. The reduction of growth rate by mucus in helioids in confinement equals the effect of high density (Herzberg, 1965; Oosterhoff, 1977; Cameron & Carter, 1979; Chevallier, 1982; Dan & Bailey, 1982). It has been claimed, however, that high density is not automatically correlated with bad living conditions (Mooij-Vogelaar et al., 1970).

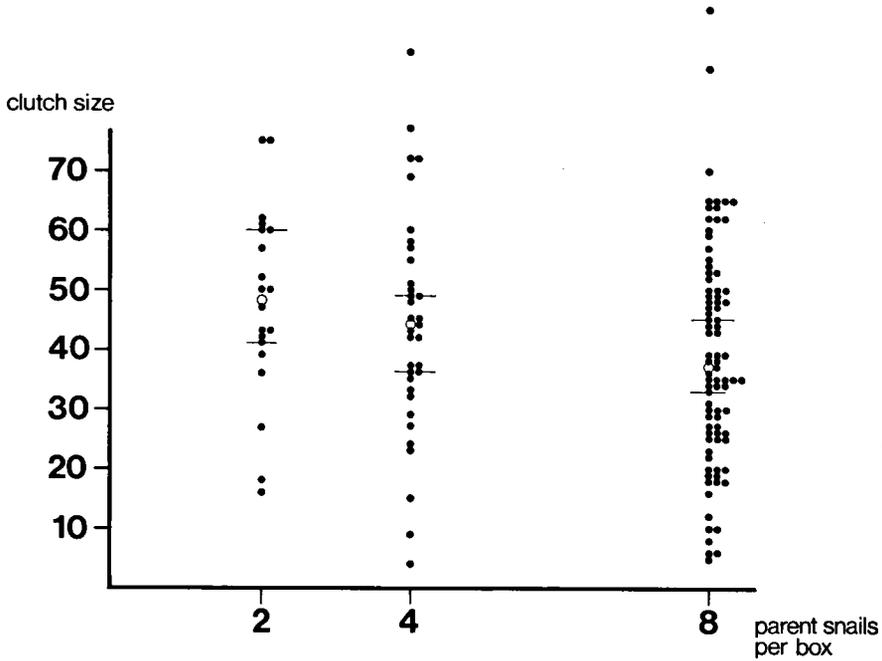


Fig. 1. Clutch size at different parental densities. A dot represents one clutch. Each circle gives the median for one parent density level. The lines limit the 95% confidence interval.

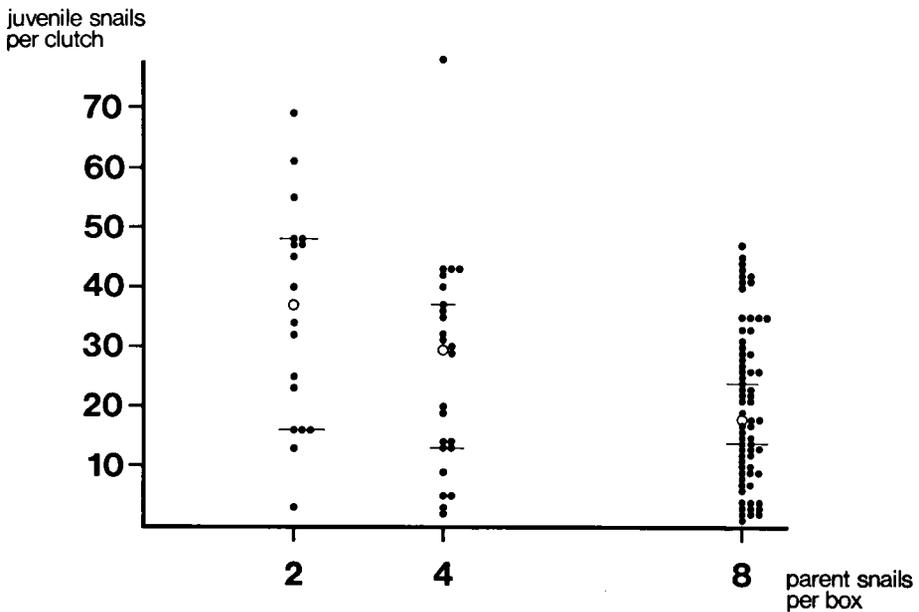


Fig. 2. Number of juvenile *Arianta arbustorum* reared from clutch at different parental densities. Dots, circles and lines as in fig. 1.

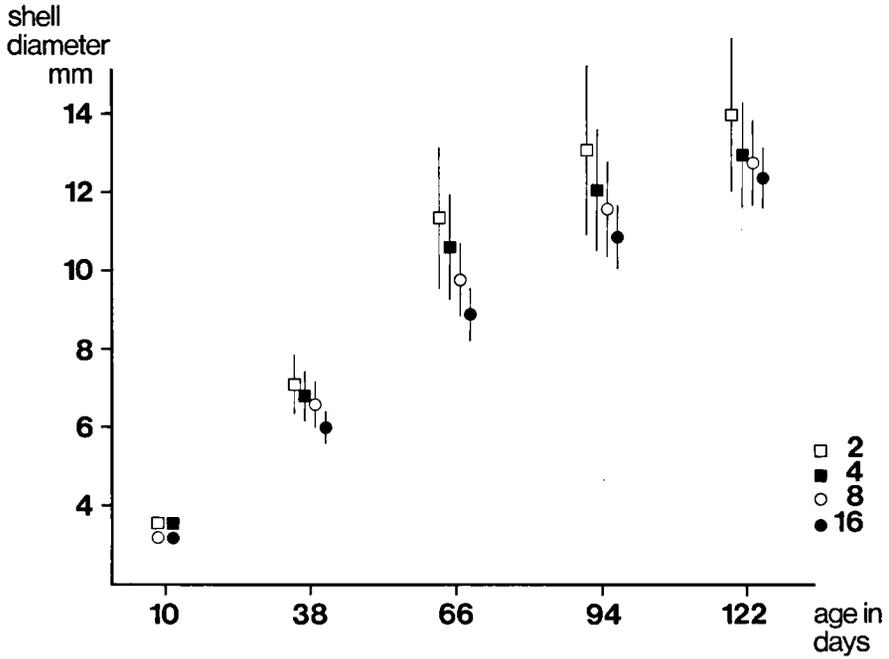


Fig. 3. Growth in juvenile *Arianta arbustorum* after hatching, at four density levels. Means with 95% confidence limits. Open square, density 2; black square, density 4; open circle, density 8; black dot, density 16.

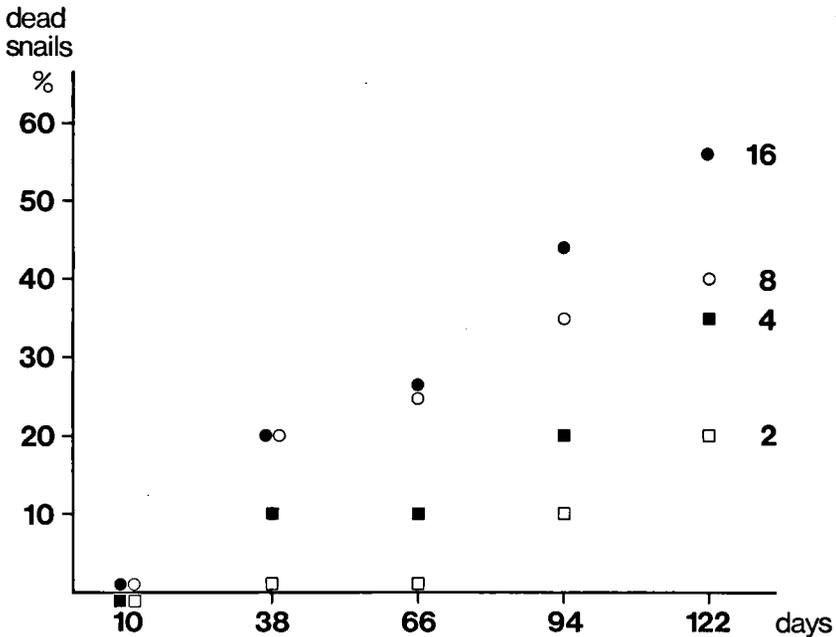


Fig. 4. Proportion of dead juvenile snails, calculated monthly for each density level separately. Symbols as in fig. 3.

9. DISCUSSION

So far, we have considered predation of and competition as regards *A. arbustorum*, but we have not shown whether predation or competition or both contribute to the regulation of population density. They do, provided their impact varies with population density. It is possible, however, that most *A. arbustorum* die of abiotic causes, just as in insects density-dependent mortality may be relatively unimportant (Rogers, 1983). If the weather is involved in regulation, it will rather be in connection with other factors or processes, such as a limited number of hiding places, or a density-related physiological change of the organisms (Klomp, 1962). Eisenberg (1966) has described regulation in *Lymnaea elodes* (Say, 1821). Russell-Hunter (1978) gives a review of molluscan populations that exhibit density-dependent control of fecundity; he suggests that more than one mechanism is involved in the regulation of density. Cain & Currey (1968) and Greenwood (1974) showed that the rate of dispersal was inversely proportional to the population density in *C. nemoralis*, and Oosterhoff (1977) claims that dispersal depends on abiotic and biotic factors as well as on individual characters like size, growth rate and morph type.

Of all the agents of regulation that can be imagined, predation seems to be the most important one. The mechanism, however, is not simple, since many different predator species are involved here. Mead (1979) mentions about 200 species preying on terrestrial snails. Many predators only take young individuals or small snail species. Wolda & Kreulen (1973) observed a juvenile mortality for *C. nemoralis* of 54 to 97.7% in the first year of their life.

In an experiment (Owen, 1980) 724 non-resident *C. nemoralis* were released in a garden. Song thrushes removed 87% of the snails within sixteen days. However, the experiment cannot be compared to native *A. arbustorum*, because they seem to know their home range and are expert at hiding. From marked *A. arbustorum* (see Baur, 1984) we know that even on rainy summer days a considerable number of the snails keep concealed, for instance by burrowing in the soil.

10. SUMMARY

Inferences were made on causes of death from the circumstances under which dead *Arianta arbustorum* or its empty shells were found. The causes included water, avalanches, heat, drought and predation by birds and mammals. In captivity *A. arbustorum* was accepted as prey by mammals and invertebrates. Population density in cages had a slightly depressing effect on both fecundity and growth, suggesting self-regulation.

11. REFERENCES

- BAUR, B., 1984. Dispersion, Bestandesdichte und Diffusion bei *Arianta arbustorum* (Mollusca, Pulmonata). — Diss. Universität Zürich: 1-89.
- BURLA, H., & W. STAHEL, 1983. Altitudinal variation in *Arianta arbustorum* (Mollusca, Pulmonata) in the Swiss Alps. — *Genetica* 62: 95-108.
- BUTLER, A.J., 1976. A shortage of food for the terrestrial snail *Helicella virgata* in South Australia. — *Oecologia* 25: 349-371.
- CAIN, A.J., & J.D. CURREY, 1968. Studies on *Cepaea*. III. Ecogenetics of a population of *Cepaea nemoralis* (L.) subject to strong area effects. — *Phil. Trans. R. Soc. London (B)* 253: 447-482.
- CAMERON, R.A.D., 1969. Predation by song thrush *Turdus ericetorum* (Turton) on the snails *Cepaea hortensis* (Mull) and *Arianta arbustorum* (L.) near Rickmansworth. — *J. Anim. Ecol.* 38: 547-553.

- , & M.A. CARTER, 1979. Intra- and interspecific effects of population density on growth and activity in some helioid land snails (Gastropoda: Pulmonata). — *J. Anim. Ecol.* 48: 237-246.
- CARTER, M.A., R.C.V. JEFFERY, & P. WILLIAMSON, 1979. Food overlap in co-existing populations of the land snails *Cepaea nemoralis* (L.) and *Cepaea hortensis* (Müll.). — *Biol. J. Linn. Soc.* 11: 169-176.
- CHEVALLIER, H., 1982. Facteurs de croissance chez des gastéropodes pulmonés terrestres paléarctiques en élevage. — *Haliotis* 12: 29-46.
- DAN, N., & S.E.R. BAILEY, 1982. Growth, mortality, and feeding rates of the snail *Helix aspersa* at different population densities in the laboratory, and the depression of activity of helioid snails by other individuals, or their mucus. — *J. moll. Stud.* 48: 257-265.
- DI CESNOLA, A.P.D., 1907. A first study of natural selection of *Helix arbustorum*. — *Biometrika* 5: 387-399.
- EBLE, H., 1963. Ernährungsbiologische Untersuchungen an *Turdus philomelos* Brehm, *Turdus merula* und *Sturnus vulgaris* L. — *Wiss. Z. Univ. Halle Math.-Nat.* 12: 211-234.
- EISENBERG, R.M., 1966. The regulation of density in a natural population of the pond snail, *Lymnaea elodes*. — *Ecology* 47: 889-906.
- FROEMMING, E., 1937. Das Verhalten von *Arianta arbustorum* L. zu den Pflanzen und höheren Pilzen. — *Arch. Moll.* 69: 161-169.
- , 1954. *Biologie der mitteleuropäischen Landgastropoden*: 1-404. Berlin.
- GRAINGER, J.N.R., 1969. Heat death in *Arianta arbustorum*. — *Comp. Biochem. Physiol.* 29: 665-670.
- GREENWOOD, J.J.D., 1974. Effective population numbers in the snail *Cepaea nemoralis*. — *Evolution* 28: 513-526.
- GRIME, J.P., & G.M. BLYTHE, 1969. An investigation of the relationship between snails and vegetation at the Winnats Pass. — *J. Ecol.* 57: 45-66.
- , —, & J.D. THORNTON, 1970. Food selection by the snail *Cepaea nemoralis* L. In: A. WATSON, 1970, *Animal populations in relation to their food resources*: 73-99. *Brit. Ecol. Soc. Symp.* 10. London, Edinburgh.
- HERZBERG, F., 1965. Crowding as a factor in growth and reproduction of *Helix aspersa*. — *Amer. Zool.* 5: 254.
- HOWES, N.H., & R.B. WHELLOCK, 1937. A semi-synthetic diet for *Helix pomatia*. — *Biochem. J.* 31: 1489.
- KLOMP, H., 1962. The influence of climate and weather on the mean density level, the fluctuations and the regulation of animal populations. — *Arch. néerl. zool.* 15: 68-109.
- LINDQUIST, B., 1941. Experimentelle Untersuchungen über die Bedeutung einiger Landmollusken für die Zersetzung der Waldstreu. — *K. Fysiogr. Sällsk. Lund. Forh.* 11: 144-156.
- MASON, C.F., 1970. Food, feeding rates and assimilation in woodland snails. — *Oecologia* 4: 358-373.
- MEAD, A.R., 1979. Biological control of terrestrial snails. — *Haliotis* 8: 263-264.
- MOOIJ-VOGELAAR, J.W., J.C. JAGER, & W.J. VAN DER STEEN, 1970. The effect of density changes on the reproduction of the pond snail *Lymnaea stagnalis* (L.) — *Neth. J. Zool* 20: 279-288.
- MORRIS, D., 1954. The snail eating behaviour of thrushes and blackbirds. — *Br. Birds* 47: 33-49.
- MURDOCH, W.W., & A. OATEN, 1975. Predation and population stability. — *Adv. ecol. Res.* 9: 1-131.
- OOSTERHOFF, L., 1977. Variation in growth rate as an ecological factor in the landsnail *Cepaea nemoralis* (L.) — *Neth. J. Zool.* 27: 1-132.
- OWEN, D.F., 1980. *What is ecology?* 2nd ed.: 1-234. Oxford.
- PARKIN, D.T., 1971. Visual selection in the land snail *Arianta arbustorum*. — *Heredity* 26: 35-47.
- , 1973. A further example of natural selection on phenotypes of the land snail *Arianta arbustorum*. — *Biol. J. Linn. Soc.* 5: 221-233.
- POLLARD, E., 1975. Aspects of the ecology of *Helix pomatia* L. — *J. Anim. Ecol.* 44: 305-329.
- POTTS, D.C., 1975. Persistence and extinction of local populations of the garden snail *Helix aspersa* in unfavourable environments. — *Oecologia* 21: 313-334.

- RAUT, S.K., & K.C. GHOSE, 1981. Factors influencing mortality in land snails, *Achatina fulica* Bowdich and *Macrochlamys indica* Godwin-Austen during aestivation. — Proc. zool. Soc. Calcutta 32: 107-120.
- REICHHOLF, J., 1979. Gefleckte Schnirkelschnecken, *Arianta arbustorum*, als Nahrung der Singdrossel *Turdus philomelos*, im Auenwald: Selektive Grössen- und Typenwahl. — Bonn. zool. Beitr. 30: 404-409.
- RICHARDSON, A.M.M., 1974. Differential climatic selection in natural population of land snail *Cepaea nemoralis*. — Nature 247: 572-573.
- , 1975. Winter predation by thrushes, *Turdus ericetorum* (Turton) on a sand dune population of *Cepaea nemoralis* (L.). — Proc. Malac. Soc. London 41: 481-488.
- ROGERS, D., 1983. Pattern and process in large-scale animal movement. In: I.R. SWINGLAND, & P.J. GREENWOOD, The ecology of animal movement: 160-180. Oxford.
- RUSSELL-HUNTER, W.D., 1978. Ecology of freshwater pulmonates. In: V. FRETTER, & J. PEAKE, Pulmonates 2A: 335-383. London, etc.
- SKORPING, A., & O. HALVORSEN, 1980. The susceptibility of terrestrial gastropods to experimental infection with *Elaphostrongylus rangiferi* Mitskevich (Nematoda: Metastrongyloidea). — Z. Parasitenkd. 62: 7-14.
- TATTERSFIELD, P., 1981. Density and environmental effects on shell size in some dune snail populations. — Biol. J. Linn. Soc. 16: 71-81.
- WAGGE, L.E., 1952. Quantitative studies of calcium metabolism on *Helix aspersa*. — J. exp. Zool. 120: 311-342.
- WILLIAMSON, M.H., 1958. An apparently simple case of population control. — Nature 182: 1008.
- WILLIAMSON, P. & R.A.D. CAMERON, 1976. Natural diet of the landsnail *Cepaea nemoralis*. — Oikos 27: 493-500.
- , —, & M.A. CARTER, 1977. Population dynamics of the land snail *Cepaea nemoralis* (L.): a six year study. — J. Anim. Ecol. 46: 181-194.
- WOLDA, H., 1963. Natural populations of the polymorphic land snail *Cepaea nemoralis* (L.). — Arch. Néerl. Zool. 15: 381-471.
- , 1965. The effect of drought on egg production in *Cepaea nemoralis*. — Arch. Néerl. Zool. 16: 387-399.
- , & D.A. KREULEN, 1973. Ecology of some experimental populations of the land snail *Cepaea nemoralis* (L.). II. Production and survival of eggs and juveniles. — Neth. J. Zool. 23: 168-188.
- , A. ZWEEP, & K.A. SCHUITEMA, 1971. The role of food in the dynamics of populations of the landsnail *Cepaea nemoralis*. — Oecologia 7: 361-381.