

SHELL PREDATION AND CANNIBALISM IN LAND SNAILS LIVING ON ACID AND CALCIUM-DEFICIENT SOILS

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ABSTRACT: Taking up calcium contained in the shells of dead snails or bird eggs is a common phenomenon in land snails. However, calcium deficiency can lead to uptake of calcium contained also in shells of live snails. At several sites we have observed *Cepaea nemoralis* gnawing at shells of live *Helix pomatia* and other *Cepaea nemoralis*. Sometimes the intensity of this behaviour was such that shells of virtually all live snails in a population, irrespective of their age, were damaged and in some cases holes through the shells could be seen. Those populations lived on acid (pH 3.6–5.9) and calcium-deficient soils (calcium content 96–774 mg/kg). Acid precipitation is recognised as one of the most important threats to terrestrial gastropods. Presently, with growing acidification of the environment, shell predation and cannibalism can be expected to occur more and more often and pose an additional threat to snail populations.

KEY WORDS: acid precipitation, *Cepaea nemoralis*, shell damage, snail behaviour

Cannibalism, defined as intraspecific predation, has been described in various gastropods (see BAUR 1992 for review). Although it has not been observed in highly specialised predators, in generalist predators it often occurs opportunistically as a consequence of the lack of specificity of predation. Herbivorous snails show a strong preference for high-nitrogen food and in those species, scavenging on carrion, including conspecifics, has been frequently observed (BAUR 1992). In hatchlings, egg cannibalism can occur, providing young snails with energy and various nutrients, including calcium. This behaviour is commonly age-specific and does not occur past the hatchling stage (BAUR 1992, HELLER 2001). In juvenile and adult gastropods, calcium is taken up with consumed food and directly from the substratum. Calcium is essential for the snails throughout their life, although predominantly during their growth stage (OOSTERHOFF 1977). Sources of calcium such as shells of dead snails or shells of bird eggs are readily used by snails, especially in calcium-deficient areas (e.g. ROST 1952, BLEAKNEY 1966, OWEN & BENGTON 1972). In some populations, however, not only dead shells but also shells of live snails can be eaten. This behaviour, associated with calcium shortage has been

observed in *Cepaea nemoralis* experimental garden enclosure populations (WOLDA 1972) and in the laboratory (OOSTERHOFF 1977). It has also been noted in a wild population of *Cepaea hortensis* in Iceland (OWEN & BENGTON 1972) and in *Achatina fulica* individuals kept on a calcium-free substrate (VOELKER 1959, WÄREBORN 1970). Here we present observations of shell predation and cannibalism in several wild populations of *Cepaea nemoralis* and relate the occurrence of this behaviour to pH and calcium content of the soil.

In July 2005 in Jessern near Lübben/S (eastern Germany) at the edge of a pine forest grown with robinia, we have observed an unusual snail behaviour. What attracted attention in the first place, was the exceptional intensity with which shells of dead snails were eaten. In many places aggregations of several *Cepaea nemoralis*, mostly juvenile, were actively radulating remnants of snail shells (Fig. 1A). Further inspection of this site revealed that shells of live snails were also intensively eaten. The snails that were preyed upon were moving around freely (Fig. 1B) or were stationary, e.g. because they were laying eggs. We observed a number of *Helix pomatia* individuals immobilised in this way whose shells were gnawed at by several *Cepaea nemoralis* at a time (Fig. 1C). Detaching



Fig. 1. Shell predation and cannibalism in *Cepaea nemoralis*. A – *C. nemoralis* gnawing at the remnants of a *Helix pomatia* shell; B – *C. nemoralis* gnawing at a shell of a live *H. pomatia*; C – *C. nemoralis* gnawing at a shell of *H. pomatia* immobilised during egg-laying; D – adult and juvenile *H. pomatia* with characteristic signs of having been gnawed at by other snails; E – shells of *C. nemoralis* damaged by conspecifics; sealing of shells from inside can be seen (all snails were alive at collection); F – *C. nemoralis* individual with a perforated shell (photo: M. Ożgo)

the predator revealed substantial damage to the shell (Fig. 1D), sometimes resulting in its perforation (Fig. 1E, F). According to our observations, when a shell of a live snail is eaten, the place attacked most often is the apex or the last whorl close to the suture. In contrast, when a snail eats an empty shell, it usually starts from the inside, just behind the lip. As a result, holes in the calcium layers are produced, but the periostracum is often left undamaged.

Subsequently we found other populations of *Cepaea nemoralis* where shells of live snails were damaged in a way characteristic of being gnawed at by other snails. One of those populations was in eastern Germany (Plötzky near Magdeburg) and four in northern Poland (Czersk, Mosty, Sławno, and Wejherowo). In some of them shells of virtually all snails irrespective of their age were damaged and in some cases holes through the shell could be observed; same of those perforations were sealed from inside (Fig. 1E, F).

All populations in which we observed shell predation and/or cannibalism lived on acid and calcium-deficient soils. The pH of the upper layer of the soil measured in KCl ranged from 3.6 to 5.9 (measured in H₂O from 4.5 to 6.2); calcium content ranged from 96 to 774 mg/kg (chemical analyses were carried out by the Chemical-Agricultural Station in Koszalin). We did not observe this behaviour in any of the *Cepaea nemoralis* populations living on less acidic and more calcium-rich soils (Fig. 2).

Acid precipitation is recognised as one of the most important threats to terrestrial gastropods, as it results in the removal of calcium from the litter and upper soil layers and renders it unavailable to snails. The number of land snail species and their abundances are correlated with pH and calcium content (BURCH 1955, VALOVRTA 1968, WÄREBORN 1970, POKRYSZKO 1993). In areas where acid precipitation causes a decrease in calcium content, progressive decrease in both species richness and abundance, up to a complete disappearance of malacofauna is observed (PAWŁOWSKA & POKRYSZKO 1998, and citations therein).

Shell predation, including cannibalism, is a behavioural response of snails to extreme calcium deficiency. With growing acidification of the environment this kind of behaviour can be expected to occur more and more often. Its effect is no doubt detrimental, as snails with large parts of the surface of their shells damaged are more liable to desiccation and, when complete perforation occurs, also to infection. Additionally, growth rates and fecundity can be reduced as a consequence of energy diverted into shell repair (RIBI et al. 1986).

It is not certain if shell predation and cannibalism occur in all snail species as a response to calcium deficiency. Our preliminary observations suggest that they might not. In Jessern where we could directly observe this kind of behaviour, *Cepaea nemoralis* predated on *Cepaea nemoralis* and on *Helix pomatia*, but we have not observed *Cepaea nemoralis* predated on *Arianta arbustorum*, nor *Helix pomatia* or *Arianta arbustorum* predated on any live snails. Similar relations were observed by Professor ADOLF RIEDEL in Brwinów near Warsaw. There, *Cepaea nemoralis* radulated shells of live *Cepaea nemoralis* and *Helix pomatia*, whereas neither *Helix pomatia*, nor *Cepaea hortensis* or *Arianta arbustorum* did radulate shells of any live snails (ADOLF RIEDEL, personal communication 2006). OWEN & BENGTSON (1972) observed *Cepaea hortensis* feeding on shells of their conspecifics; similar behaviour was observed by VOELKER (1959) in *Achatina fulica* in conditions of severe calcium deficiency.

Notwithstanding its negative effects, shell predation and cannibalism may be regarded as an adaptation allowing populations to persist in the conditions of limited availability of a vital resource. Individuals able to use shells of other snails, including conspecifics, as a source of calcium are possibly better fit to survive and reproduce than others. *Cepaea nemoralis*, *Cepaea hortensis* and *Achatina fulica* are successful colonisers of novel environments. Shell predation and cannibalism may be one of the adaptations allowing populations of those species to persist in spite of very unfavourable conditions.

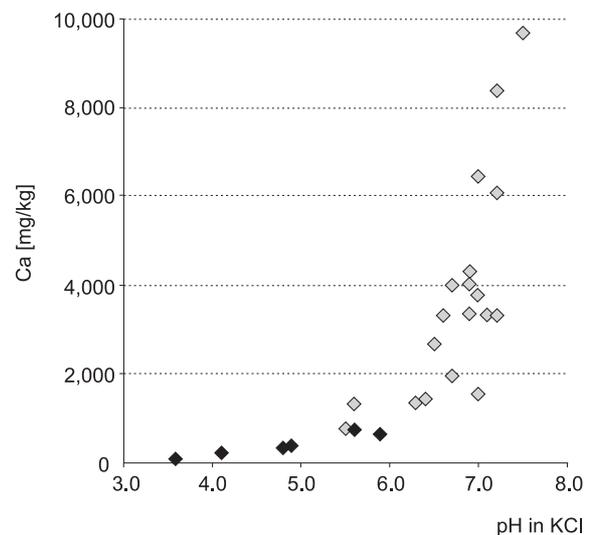


Fig. 2. Soil pH and calcium content at sites inhabited by *Cepaea nemoralis*. Black diamonds – populations where shell predation/cannibalism occurred

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