J. Moll. Stud. (1991), 57: 331-336.

THE EFFECT OF HIBERNATION POSITION ON WINTER SURVIVAL OF THE ROCK-DWELLING LAND SNAILS *CHONDRINA CLIENTA* AND *BALEA PERVERSA* ON ÖLAND, SWEDEN

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(Received 29 May 1990, accepted 17 September 1990)

ABSTRACT

The effect of hibernation position on winter survival was examined for four years in the rock-dwelling land snails *Chondrina clienta* and *Balea perversa* inhabiting exposed stone walls on the Baltic island of Öland, Sweden. Individuals of both species hibernated either singly or aggregated in groups, attached to the lower surface of horizontally arranged pieces of limestone. *B. perversa* hibernated more frequently in aggregations than did *C. clienta*, and in both species adults occurred more frequently in aggregations than did juveniles. For both age classes of *C. clienta* in winter 1987/88 and for juveniles of *B. perversa* in 1988/89, individuals that hibernated in large aggregations had a higher survival rate than individuals hibernating singly or in small aggregations. No differential survival with respect to hibernation position was found in the winter of 1986/87 when the lowest temperatures were recorded (minimum temperature −16.4°C). During this extremely cold winter mean survival rates of 33.9% were recorded for *C. clienta* and 73.3% for *B. perversa*. The succeeding three winters were mild, with mean survival rates of 83.2% in *C. clienta* and 91.1% in *B. perversa*. In both species adults had a higher survival rate than juveniles. After a period of extreme cold (−16°C) survival of *C. clienta* inhabiting a snow-covered pile of stones was significantly higher than that of conspecifics on a snow-free stone wall, suggesting that snow cover has an insulating effect.

INTRODUCTION

Unfavourable weather is known to act as a density-independent mortality factor in many invertebrate species (Andrewartha & Birch, 1954; Price, 1984; Begon, Harper & Townsend, 1986). Winter survival is assumed to be one of the crucial factors in the life cycle of land snails (Wolda, 1963; Wolda & Kreulen, 1973; Cain, 1983). Land snails overwintering at or near the soil surface in temperate regions are potentially exposed to low temperatures, being readily killed by ice formation in the tissue (Stöver, 1973; Riddle, 1983). Consequently, behavioural adaptations (e.g., searching for favourable hibernation positions) and physiological acclimatization, such as the development of cold-hardiness in autumn prior to the appearance of insulating snow layers and the maintenance of sufficient cold resistance during winter, may be essential in such species (Riddle, 1981; Riddle & Miller, 1988).

Here we report on winter survival as a function of hibernation positions in two species of rock-dwelling land snails, *Chondrina clienta* (Westerlund, 1883) and *Balea perversa* (L., 1758), on the Baltic island of Öland, Sweden. The species co-occur in stone walls, where they are exposed to ambient temperatures and winds during hibernation. The following questions were addressed: (1) do species and age classes differ in their hibernation positions? (2) does snail survival depend on the hibernation position? and (3) does survival differ among species and age classes? Furthermore, to examine the effect of snow cover, we compared the survival of individuals inhabiting an exposed stone wall and a snow-covered stone pile following a period of extreme cold.

Chondrina clienta occurs in open limestone areas of central and south-eastern Europe and in three isolated areas of Sweden, namely on the Baltic islands of Öland and Gotland and a small area on the mainland (Kerney & Cameron, 1979; Gittenberger, 1984; Waldén, 1984; Baur, 1987). Its cylindro-conical shell is dextral and in adults is 5.5-7 mm high (Kerney & Cameron, 1979; Baur, 1988). *Balea perversa* is a species characteristic of dry places among rocks and old stone walls, occurring occasionally on stems of trees, and is widely distributed in western Europe, in Scandinavia mainly along the coast, and up to 68°N in Norway (Boycott, 1921; 1934; Kerney & Cameron, 1979). Its narrowly conical shell is sinistral and in adults is 7-10 mm high (Kerney & Cameron, 1979). Both species are particularly well adapted to rocky habitats; they are very resistant to drought (cf. Neuckel, 1981), and their specialized radulae enable them to graze epi- and endolithic lichens (the snails' exclusive food resource) from rock surfaces (Schmid, 1929; Breure & Gittenberger, 1982). It has been experimentally demonstrated that *C. clienta* and *B. perversa* are involved in both intra- and interspecific competition (Baur, 1990; Baur & Baur, 1990).

MATERIALS AND METHODS

Specimens of *C. clienta* and *B. perversa* were collected from stone walls at five sites in the heath-grassland Stora Alvaret in the southern part of the Baltic island of Öland, Sweden (56°33'N, 16°36'E), in late March/early April 1987-1990. The stone walls considered in this study are made of flat pieces of limestone arranged in horizontal layers. Individuals of both species overwinter in gaps between the limestone slabs. The resting position of each snail found on the lower surface of randomly selected stones was classified into one of the following categories: (1) occurring singly, (2) occurring in a small aggregation (3-10 individuals in close proximity), and (3) occurring in a large aggregation (> 10 individuals). In addition, for 1987/88 and 1989/90 each snail found was classified as hibernating either on the flat stone surface or in a small depression on the stone surface. Only individuals with an intact periostracum covering their shells were considered; it can be assumed that these animals were alive in the preceding autumn. Data were collected for both juveniles and adults of each species. Fully-grown snails (individuals with teeth at the shell aperture in *C. clienta* or with a reflected lip in *B. perversa*) or nearly fully-grown snails (approximately the same size as fully-grown individuals but without teeth or a reflected lip) were regarded as adults, and all others as juveniles.

To estimate actual snail densities, the number of hibernating snails counted was divided by the lower surface area of the pieces of limestone (no density estimates were made in winter 1986/87).

To determine snail survival, individuals were collected and placed on moist paper towels in covered plastic containers in the laboratory at approximately 21°C; animals that did not awake during the first 24 hours were considered dead.

To examine whether an abundant snow cover insulated hibernating animals, snail survival following a period of extreme cold was determined for two differently exposed habitats on 3 January 1987: (1) a stone wall (approximately 90 cm high) was completely exposed, and (2) a pile of stones (4 m × 25 m wide, 1 m high) covered by 25 cm of snow. The two habitats were separated by a 4 m wide grass strip. Snail samples comprised all individuals attached to nine randomly chosen stones in the wall and to 15 stones in the stone pile. At the time of collection, air temperature was −8°C, but had dropped as low as −16°C the preceding nights. Snail survival was determined as described above. Shell size (maximum height) of all snails was measured using a binocular microscope with a stage micrometer. Comparisons of snail density between the two habitats were based on stones of similar size.

Temperature data were obtained from the Meteorological Station near Ölands Södra Udde, located 30 km south of the investigation sites (Anonymous, 1986-1990). If not mentioned otherwise, statistical analyses were applied only when the snail groups consisted of at least 50 individuals.

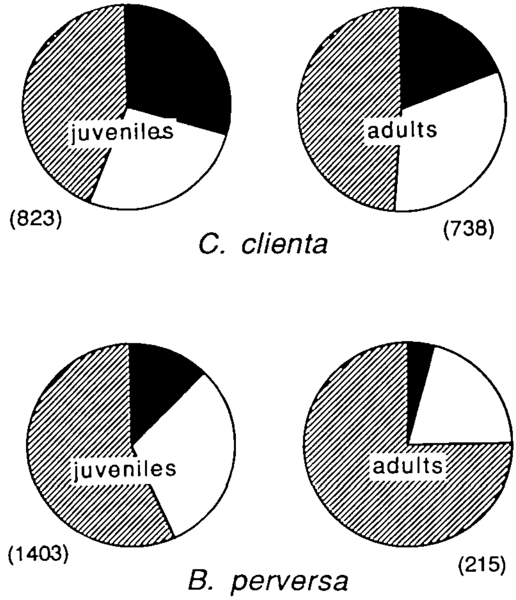

Figure 1. Proportions of juvenile and adult *C. clienta* and *B. perversa* hibernating ■ singly, □ in small aggregations, and ▨ in large aggregations on stone walls. Data for the four winters are pooled and number of snails examined are indicated in parenthesis.

RESULTS

Hibernation positions in stone walls

Hibernation positions were recorded for 1561 individuals of *C. clienta* and 1618 individuals of *B. perversa* over 1987-1990. The snails hibernated most frequently between pieces of stones. For both species, the proportions of individuals occurring singly, in small aggregations and in large aggregations, respectively, are illustrated in Fig. 1. The species differed in their hibernation positions: 88.4% of all *B. perversa* occurred in aggregations compared with 75.3% of *C. clienta*. In both species juveniles and adults

Table 1. Winter survival of juveniles and adults of *C. clienta* and *B. perversa* in stone walls on Öland 1987-1990 and temperatures recorded. Mean winter temperature refers to the average of daily mean temperature in the period December-March. N indicates the number of snails examined per species and age group.

Winter	*C. clienta* Juveniles		*C. clienta* Adults		*B. perversa* Juveniles		*B. perversa* Adults		Mean winter temperature*	Minimum winter temperature	
	%	N	%	N	%	N	%	N	°C	°C	Date
1986/87	35.7	(14)	32.1	(28)	61.9	(806)	84.7	(98)	−2.3	−16.4	11 Jan. 87
1987/88	85.6	(348)	94.1	(406)	94.4	(36)	100.0	(1)	2.0	−5.2	8 Feb. 88
1988/89	76.0	(25)	77.1	(35)	73.9	(134)	96.0	(25)	3.0	−7.4	21 Nov. 88
1989/90	96.6	(436)	97.4	(269)	93.9	(269)	96.7	(91)	4.0	−11.5	16 Dec. 89

* average from 1931-1960: 0.4°C

preferred different hibernation positions (χ^2-test, in both species, $P < 0.001$; Fig. 1), with juveniles occurring singly more frequently than adults. Furthermore, compared to adults, juveniles of *C. clienta* showed a significant preference for hibernating in depressions of the stone surface (χ^2-test, $P < 0.001$).

Winter survival

Winter survival rates of juveniles and adults of *C. clienta* and *B. perversa* are presented in Table 1. For all age groups and species survival rates were lowest in winter 1986/87, when the lowest minimum temperature was recorded (that winter was 2.7°C colder than an average winter; Table 1). The following three winters were mild and significantly higher survival rates were recorded for both species (winter 1989/90 was the warmest of this century (Anonymous, 1990)). Considering all four years, winter survival of *C. clienta* averaged 89.1% in juveniles and 92.1% in adults. Corresponding figures for *B. perversa* were 73.6% in juveniles and 91.2% in adults. In the winter 1986/87 significantly more adults of *B. perversa* survived than juveniles (χ^2-test, $P < 0.001$; Table 1), indicating an age-specific mortality. Similarly, in the winter 1987/88 significantly more adults of *C. clienta* survived than juveniles (χ^2-test, $P < 0.001$; Table 1).

Winter survival appeared to be density-independent. No correlation between density of hibernating snails and percentage of survivors was found in either species and age class.

Survival in relation to hibernation position

Statistical tests for differential survival among categories of dispersion were carried out separately for juvenile and adult individuals of *C. clienta* in winter 1987/88, for both age classes of *B. perversa* in 1986/87 and for juveniles of *B. perversa* in 1988/89 (in winter 1989/90 mortality was too low to perform any statistical tests). In *C. clienta*, individuals of both age classes had a significantly higher survival rate when they hibernated in large aggregations than in small aggregations or singly (χ^2-test, for both age classes, $P < 0.02$). Similarly, juveniles of *B. perversa* in large aggregations survived the winter of 1988/89 better than those hibernating in small aggregations or singly (χ^2-test, $P < 0.01$). However, in the extremely cold winter 1986/87 no differential survival was found in either age class of *B. perversa*, no matter whether they hibernated in aggregations or were singly dispersed (χ^2-test, for both groups, $P > 0.2$).

Statistical tests for differential survival among snails hibernating on the flat stone surface vs. those in small depressions were carried out for juvenile and adult individuals of *C. clienta* in 1987/88 and for juveniles of both species in 1989/90. In none of these cases was any difference in survival found (χ^2-test, in all cases $P > 0.05$).

Survival in differently exposed habitats

For a sample of 575 snails collected after a period of extreme cold on 3 January 1987, Table 2 gives the percentage of each species that had survived in each habitat. Significantly more *C. clienta* survived in the snow-covered stone pile than in the exposed wall (χ^2-test, $P < 0.01$), suggesting an insulating effect of the snow cover. No corresponding comparison can be made for *B. perversa*, since only one individual was found in the stone pile.

Table 2. Percentage of individuals of *C. clienta* and *B. perversa* that survived a period of extreme cold (−16°C) in differently exposed habitats in winter 1986/87 on Öland.

Species Age class	Habitat			
	Exposed stone wall		Snow-covered stone pile	
	%	N	%	N
C. clienta				
Juveniles	69.2	(26)	82.4	(165)
Adults	84.3	(51)	95.1	(246)
Juveniles + Adults	79.2	(77)	90.0	(411)
B. perversa				
Juveniles	71.4	(35)	100.0	(1)
Adults	100.0	(51)	-	(0)
Juveniles + Adults	88.4	(86)	100.0	(1)

Comparing age classes within species, a significantly larger proportion of adult than juvenile *B. perversa* survived in the stone wall (χ^2-test, $P < 0.001$). Similarly, a slightly higher proportion of adult *C. clienta* survived in the stone wall than did juveniles, but the difference was not significant (χ^2-test, $P = 0.13$). In the stone pile, adult *C. clienta* had a significantly higher survival rate than juveniles (χ^2-test, $P < 0.001$).

The density of *C. clienta* was significantly lower in the wall (8.6 individuals per stone) than in the stone pile (27.4 individuals per stone) (Mann-Whitney *U*-test, $P < 0.001$). Individuals in the wall were on average larger (shell height of adults: 6.4 ± 0.2 mm [mean $\pm$ S.D.], $N = 23$) than those in the stone pile (5.6 ± 0.2 mm, $N = 216$). However, no difference in size between survivors and non-survivors was found among adults in either habitat (Mann-Whitney *U*-test, $P > 0.1$ in both cases). This indicates that the shell-size difference of *C. clienta* inhabiting the contrasting habitats is not a result of size-selective mortality among adults.

DISCUSSION

Behavioural aspects of hibernation that influence survival have received little attention in land snails. Carney (1966) observed that individuals of *Allogona ptychophora* (Brown) hibernating with their aperture facing downwards suffered a higher mortality than others, while the opposite was found in *Arianta arbustorum* (L.) (Terhivuo, 1978). In the present study, hibernating *C. clienta* and *B. perversa* were found mainly in gaps between horizontal layers of pieces of limestone. The finding that individuals hibernating in large aggregations had the highest survival (in the winters 1987/88–1989/90) suggests that these individuals had found particularly suitable places to spend the winter, where they may be sheltered against the direct impact of wind. By contrast, snails hibernating on the outer surface of a stone wall are more exposed to ambient temperature and wind, but are in closer proximity to abundant food resources (lichen). In view of the keen intra- and interspecific competition for food (Baur, 1990; Baur & Baur, 1990), the snails may be faced with a trade-off between sheltered resting sites suitable for hibernation (crevices or depressions on the lower surface of stones) and ones near abundant food resources (lichen on the upper surface of stones). Schlesch (1937) observed *C. clienta* grazing lichen under mild conditions in January on Öland. Thus, winter dormancy is not deep in these rock-dwelling species. In this context it is interesting that both species did occur in the same aggregations.

After abundant snowfall, snails living in habitats where snow accumulates (e.g. stone piles) are insulated against very low temperatures, irrespective of their actual position, whereas snails inhabiting exposed stone walls run a greater risk of mortality from low temperatures. On the other hand, the stone walls may provide more food to snails. Breeding birds (e.g. wheatears, *Oenanthe oenanthe*) frequently use stone walls as perching sites in this extremely flat grassland and, as a result, the uppermost pieces of stones are patchily covered with droppings (Fröberg, 1989; A. Baur & B. Baur, pers. observations). During rainfall nitrogenous, phosphorous and other substances in the bird faeces are dissolved and spread over larger areas of the walls, thereby enhancing the growth of lichens (Fröberg, 1989). Thus the disadvantage to snails of being exposed to low temperatures and winds may be counteracted by a relatively high growth rate of their food.

The minimum lethal temperatures for the two snail species studied here are not known, but may be below −5°C. In general, *B. perversa* survived winter slightly better than *C. clienta*, and thus probably is better adapted to cold, as indicated by the species' northern range of distribution (Kerney & Cameron, 1979). *Chondrina clienta* hibernated more shallowly in fissures and gaps between layers of pieces of limestone than did *B. perversa*, and a few individuals even spent the winter on the upper surface of stones. Thus, the hibernating behaviour of *C. clienta* may cause these snails to run a greater risk of mortality from cold.

Cold may cause a substantial part of the total mortality in land snails (Williamson, Cameron & Carter, 1977; Cain, 1983). Winter mortalities ranging from 2.4% to 19.0% have been reported for *Allogona ptychophora, A. profunda* (Say), *Mesodon thyroidus* (Say) and *Arianta arbustorum* (Blinn, 1963; Carney, 1966; Terhivuo, 1978; Andreassen, 1981). In a six-year study on the population dynamics of *Cepaea nemoralis* (L.), winter mortality among adults averaged 18% (Williamson *et al.*, 1977). All these species hibernate in leaf litter or dig into the soil, which contrasts with *C. clienta* and *B. perversa* that hibernate on rock-faces. Yet, *C. clienta* and *B. perversa* did not suffer significantly higher mortalities than the other species mentioned, suggesting that these rock-dwelling land snails have very efficient adaptations to cold. Oosterhoff (1977) found that winter mortality in *Cepaea nemoralis* is age-specific, affecting most frequently the smallest individuals. Similarly, in both *C. clienta* and *B. perversa*, smaller individuals died more frequently than did larger ones, suggesting that adult snails can better withstand cold.

Cold can act as a density-independent mortality factor in terrestrial gastropods. Decreases in individual number after severe frosts have been found in natural populations of the slugs *Deroceras reticulatum* (Müller) and *Arion hortensis* Férussac (South, 1965; Hunter, 1966). Similarly, winter survival of *C. clienta* and *B. perversa* tended to decrease—irrespective of local population size—with decreasing minimum temperature.

A decrease in adult shell size with increasing population density has been recorded in several land snail species (reviewed by Goodfriend, 1986), but all evidence points to a direct environmental influence of density on shell size, rather than a size-selective effect. Baur (1988) found that adult shell size of *C. clienta* decreased with increasing local population density and Baur & Baur (1990) demonstrated experimentally that intra- and interspecific competition affect adult shell size in both snail species. Thus, the difference in adult size among individuals living in the exposed and the sheltered (snow-covered) habitat may be due to competition for food rather than to size-selective winter mortality.

To conclude, this study showed that winter temperatures influence snail survival and that juveniles of both *C. clienta* and *B. perversa* suffer higher mortality than adults. Furthermore, winter survival can to some extent be enhanced by behavioural adaptations, such as search for particularly suitable hibernation positions.

ACKNOWLEDGEMENTS

We thank the staff at the Ecological Research Station of Uppsala University on Öland for their hospitality, S. Larsson for field assistance and H. Dobson and S. Ulfstrand for constructive comments on the manuscript. Financial support was received from The Swedish Royal Academy of Sciences (to A.B.) and the Swiss National Science Foundation (to B.B.).

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