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Selection for adult shell size in natural populations of the landsnail Cepaea hortensis (Müll.)

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Samples of adults of the snail *Cepaea hortensis* (Müll.) from natural populations in southern Iceland were analysed with respect to variation in shell diameter. Significant differences in mean shell size occurred between areas and closely adjacent sites. Analyses of June samples from different sites within a restricted area revealed a significant association ($P \sim 0.01$) between mean shell size, mean minimum temperature, calcium in soil, and calcium in decaying vegetation, temperature accounting for most of the variation in shell size. Variation within samples was small, with coefficients of variation ≤ 5 %.

At a site studied for 5 years seasonal and annual variations in mean shell size were small. Between consecutive sampling occasions some significant changes in variance occurred, mostly during summer and autumn when recruitment of adults takes place. In some winters a significant reduction of variance occurred, which suggests stabilizing selection. During winters the mean shell size decreased, although not statistically significantly. However, the mean shell size in early June was positively correlated with the air temperature of the preceding winter ($P = 0.017$). It is suggested that the mean shell diameter of the adult snails is subject to climatic selection.

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1. Introduction

Mean shell size of adult individuals of terrestrial snails of *Arianta arbustorum* (L.) and the genus *Cepaea* varies geographically but also between closely adjacent, and ecologically similar, sites (e.g. Lamotte 1951, Röst 1952, Cook 1965, Wolda 1969, Cook & O'Donald 1971). Laboratory studies on *Cepaea nemoralis* (L.) and *A. arbustorum* have established a genetic component of adult shell size ranging up to 70 % (Cook 1965, 1967, Wolda 1969, 1970, Oosterhoff 1977). Environmental factors such as temperature, humidity, calcium, and population density have been shown to affect the growth rate of juvenile *C. nemoralis*, which in turn is positively correlated with adult shell size (see Oosterhoff 1977 and references therein). Furthermore, Wolda (1963) demonstrated a positive correlation between adult shell size and the number of eggs laid. Thus, adult shell size is a relevant parameter in studies on the population dynamics of helicid snails and from the point of view of selection. Cook & O'Donald (1971) found differential mortality related to shell size in adult *C. nemoralis* hibernating in the laboratory and suggested that selection (implicit climatic selection) acting on adult individuals may optimize mean shell size and lead to differences in size between populations.

In this paper we report on spatial and temporal variation in mean shell diameter of adult *Cepaea hortensis* (Müll.) collected from natural populations in southern Iceland. Presumably some of the variation is due to genetic factors (see above for *C. nemoralis* and *A. arbustorum*) though in the following we attempt to assess environmental effects (temperature and calcium content of soil and decaying vegetation) on mean shell diameter.

2. Study areas

C. hortensis has a patchy and restricted distribution along the south coast of Iceland. The field work was carried out in two such restricted areas: (a) around the small coastal village of Vík and (b) near Drangshlið farm (Fig. 1). The south coast of Iceland has a pronounced maritime climate with relatively mild winters, cool summers, and much rainfall. For Vík the mean temperatures of the coldest and warmest months are 1.2° C (January and February) and 11.3° C (July), and the mean annual precipitation amounts to 2250 mm, rather evenly distributed over the year (Eythorsson & Sigtryggson 1971). Corresponding climatic data are not available for Drangshlið, but the geographical position and topography (cliffs facing the sea), and the composition of the invertebrate fauna (Lindroth et al. 1973) indicate that conditions are similar to those prevailing around Vík, the mean summer temperature possibly being slightly higher. Further details concerning the study areas are to be found in papers dealing with the polymorphism of *C. hortensis* (Owen & Bengtson 1972, Bengtson et al. 1976, 1979).

In both areas the snails occur in clumps of vegetation on perpendicular cliffs and at Vík also on talus slopes covered with grass and herbs (see Owen & Bengtson 1972, Bengtson et al. 1979). *C. hortensis* is frequently found in *Angelica*, *Rumex* and *Taraxacum*. Owing to differences in the size of the areas the total number of snails around Vík is much larger than at Drangshlið although the population densities are probably similar. On the slopes southwest of Vík, where *C. hortensis* has a continuous distribution, the density of adults is usually of the order of 3—6 ind m^{-2} (depending on habitat), but it was not possible to obtain reliable estimates from the small patches of vegetation on the cliffs.

Practically all our information on the general biology of *C. hortensis* in Iceland comes from observations around Vík. The snails are inactive from the end of October until April or May and hibernate in the top-layer of the soil or in the dense moss. Egg-laying occurs from June till September, no eggs being found in November. Newly hatched individuals take about 3 years to become adult and recruitment of new adults to a population occurs mainly in July and August, as indicated by the frequency of subadults (see below) and "fresh" adults in samples.

3. Material and methods

On the slopes the snails were collected by random searching in restricted patches of vegetation or by square sampling. Each sample was obtained within an area with a diameter of $\leq$ 30 m (in the following referred to as site or population) and all adult snails encountered were collected. The minimum distance between the perimeters of two sites was never less than 50 m, which we consider to exceed the size of the panmictic unit. Samples from the cliffs were randomly collected at sites which usually had an extent of about 2—5 m and were separated by sections of bare rock.

An individual is considered adult when it has formed a hard lip at the edge of the mouth of the shell, after which there is no further increase in shell diameter. Individuals of adult size in which the lip was lacking or thin and soft were classified as subadults and disregarded in this study. The size of the shell was measured as the diameter to the nearest 0.1 mm as described by Wolda (1963: fig. 1). To reduce the effects of possible changes in method all measurements were made over a short period of time and by the same person.

In both study areas effectively all *C. hortensis* are yellow coloured but highly polymorphic for banding (Owen & Bengtson 1972). Within samples, differences in shell size between morphs were rare and insignificant. Thus,

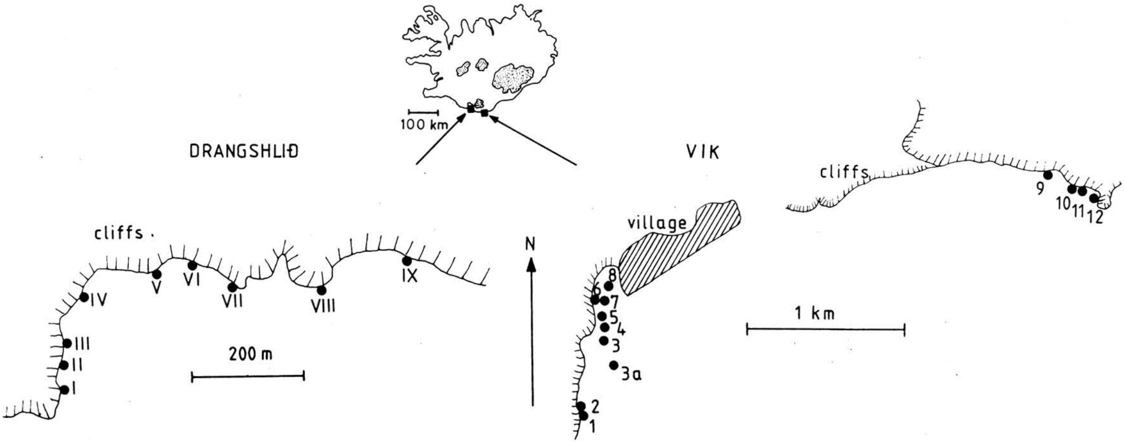

Fig. 1. Sketch maps showing the study areas (a) Vík in Myrdal (ca. 63°25'N, 19°00'W) and (b) Drangshlið (40 km W Vík) in southern Iceland. Samples of *C. hortensis* were collected at sites (black dots) on steep cliffs or talus slopes close to the sea (at Vík < 1.6 km and at Drangshlið ca. 4 km). The numbering of the sites is identical with that used in Bengtson et al. (1979).

differences between sites with respect to morph frequencies are not likely to cause any serious bias to our mean values of shell diameter (cf. Cook & O'Donald 1971).

At site number 5 on the slopes southwest of Vík (Fig. 1) the population dynamics of *C. hortensis* was studied by random square sampling three to six times each year for 5 years. This site (referred to as the monitored population) provided the main information on temporal variation in shell size.

In the first half of June 1977 we investigated 13 sites around Vík (Fig. 1) for possible correlations between mean adult shell diameter, mean daily minimum temperature (measured at +15 cm), calcium content of soil, and calcium content of decaying vegetation (on which the snails frequently feed by grazing on the surface). The temperature recordings were made during a period with a clear sky and without rainfall and are therefore thought to reflect differences between the sites. Temperature recordings in August 1977 failed to produce useful data because of heavy overcast and rain.

On 11 June 1977 samples of snails were collected at eight sites at Drangshliđ (Fig. 1). No environmental data were collected except for a sample of decaying vegetation from site VI which was analysed for calcium. Table 1 gives pertinent data for the sites around Vík and at Drangshild in June 1977. At some of the sites we had collected samples of snails earlier in the 1970s and we also had access to a snail sample obtained by the late Professor Carl H. Lindroth in 1929 at what has been positively identified as our site VI (Table 2).

4. Results

A. Differences between areas and sites

The adult *C. hortensis* from Drangshliđ were on average about 1 mm larger in shell diameter than those from Vík (Table 1). The means of the samples from Vík ranged from about 15.0 to 16.4 mm compared with 16.4 to 17.3 mm of those from Drangshliđ. Also, the shells from Vík were clearly (though not measured) more delicate than those from Drangshliđ. Analysis of variance (completely randomized design) showed that, within each of the two areas, there were differences in means between samples ($P < 0.001$). At Drangshliđ there seemed to be a clinal variation with smaller means at sites

Table 1. Mean shell diameter of adult *C. hortensis*, mean daily minimum temperature (+ 15 cm), calcium content of soil, and calcium content of decaying vegetation (a mixture of herbs, chiefly *Angelica*) at sites surveyed in the first half of June 1977 around Vík and at Drangshliđ in southern Iceland (see Fig. 1). The sites, and numbering, are identical with those discussed by Bengtson et al. (1979) but *not* with those in Owen & Bengtson (1972). The coefficient of variation (CV) is the standard deviation expressed as a percentage of the mean. No specimens from site V at Drangshliđ were measured.

Area, site	Habitat characteristics	n	Shell diameter (mm) mean	s^2	CV	Mean min. temp. C°	Ca (mg/g d wt) Soil	Vegetation
Vík:								
1	Grassy slope facing E, scattered herbs, dense moss	37	15.90	0.48	4.3	5.7	1.39	4.36
2	Slope facing E, some grass, dense herbs incl. *Angelica*	114	15.73	0.33	3.6	4.9	0.32	2.91
3	Foot of slope, mixed herbs and *Elymus*, abundant stones and moss	78	15.70	0.30	3.5	5.3	0.30	2.75
3a	Sand dunes, scattered *Elymus* and grass	10	15.94	0.36	3.8	6.0	0.23	1.55
4	Grassy slope facing E, some herbs and moss	89	15.70	0.34	3.7	5.5	0.27	4.17
5	Slope facing E, meadow rich in herb incl. *Angelica*, abundant moss	55	15.47	0.27	3.4	4.7	1.05	4.82
6	Cliff facing SE, grass and rich herbs incl. *Angelica*	78	15.55	0.28	3.4	5.6	4.98	2.07
7	Stony slope facing E, very dense *Angelica*, moss sparse	13	15.70	0.37	3.5	5.1	1.50	5.16
8	Slope facing SE, herb meadow, abundant *Angelica* and moss	56	14.98	0.29	3.6	5.2	1.78	3.79
9	Cliff facing S, abundant *Angelica* and moss	39	16.36	0.38	3.8	7.0	5.39	7.37
10	— » —	57	15.88	0.27	3.3	6.6	5.38	3.96
11	— » —	72	15.84	0.36	3.8	6.3	2.51	4.33
12	Grassy slope facing S, abundant moss	29	15.56	0.30	3.5	6.8	3.02	3.48
Drangshliđ:								
I	Cliff facing E, plenty of grass and herbs incl. *Angelica*	6	16.43	0.18	2.6	—	—	—
II	— » —	15	16.64	0.33	3.4	—	—	—
III	— » —	8	16.55	0.18	2.5	—	—	—
IV	— » —	33	16.57	0.24	3.0	—	—	—
VI	Ditto but facing S	16	17.14	0.76	5.1	—	—	10.79
VII	— » —	45	16.81	0.29	3.2	—	—	—
VIII	— » —	32	17.07	0.34	3.5	—	—	—
IX	— » —	42	17.28	0.25	2.9	—	—	—

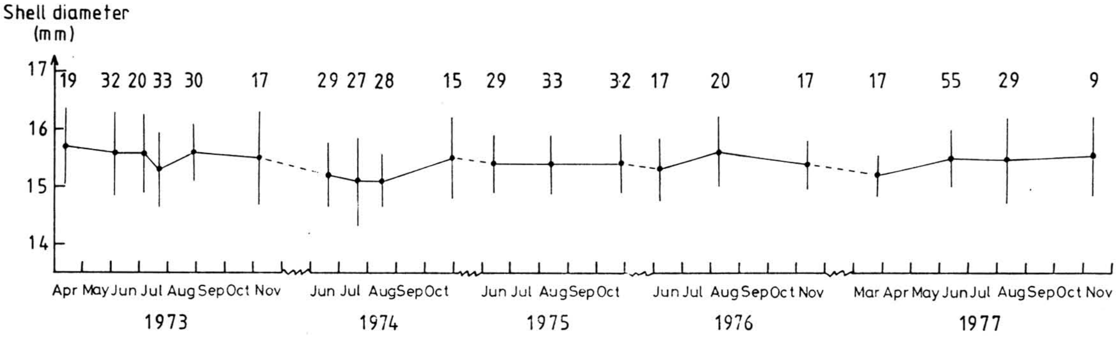

Fig. 2. Seasonal variation in mean shell diameter (± standard deviation and sample size) of adult *C. hortensis* in the population monitored at Vík, southern Iceland (site 5 in Fig. 1). The snails were obtained by square sampling, though in June 1977 additional specimens were collected at random.

I—IV (roughly facing east) than at sites VI—IX (facing south). No such trend was discernible around Vík (Fig. 1, Table 1).

B. Variation within sites

Coefficients of variation (standard deviations as percentages of means) were small, usually of the order of 3—4 % (Table 1). Shell size may vary in two ways, by changes in the mean or by changes in the variance. Figure 2 shows the temporal variation in the mean shell diameter of the population monitored at Vík during 1973—1977. The mean shell diameter remained rather stable around 15.5 mm, with no statistically significant changes between consecutive sampling occasions. Although the coefficient of variation was always ≤ 5 % in samples from the monitored population some statistically significant changes in variance occurred between consecutive sampling periods. The variance increased between August and October/November in 1973 and 1974 and between June and August in 1977 ($P < 0.05$) and decreased between July and August in 1974 ($P < 0.001$). Changes in variance approaching significance occurred between June and July in 1974 (increase). During hibernation the variance decreased in the winters of 1973/74 (0.62 to 0.30; $P < 0.05$) and 1974/75 (0.48 to 0.26; $0.1 > P > 0.05$), though not in the winters of 1975 /76 and 1976/77.

In populations studied for at least 4 years (the approximate generation period of *C. hortensis*) the mean shell diameter remained remarkably stable (Table 2). The monitored population showed some annual fluctuations (ranging between 15.22 and 15.58 mm).

Table 2. Mean shell diameter of adult *C. hortensis* in June samples of different years from sites in southern Iceland (see Fig. 1).

Area, site	Year	n	Shell diameter (mm)	
			Mean	SD
Vík:				
1	1972	133	15.85	0.59
	1977	37	15.90	0.69
3	1971	240	15.75	0.52
	1977	78	15.70	0.58
5	1973	32	15.58	0.70
	1974	29	15.22	0.55
	1975	29	15.35	0.51
	1976	17	15.29	0.53
	1977	55	15.47	0.52
9	1971	20	16.40	0.58
	1977	39	16.36	0.62
12	1971	40	15.65	0.52
	1977	28	15.56	0.54
Drangshlið:				
VI[1]	1929	7	17.27	0.62
	1973	22	17.13	0.54
	1977	16	17.14	0.87
VII	1973	37	16.85	0.56
	1977	34	16.81	0.59

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[1] Sample from 23 June 1929 collected by the late Professor Carl H. Lindroth

C. Effects of environmental factors

The association between mean shell size, mean daily minimum temperature, calcium content of soil, and calcium content of decaying vegetation in June at sites around Vík (Table 1), analysed by ranking methods that involve calculation the coefficient of concordance (W), was found to be statistically significant ($W = 0.49$, $F = 2.89$, $df_1 = 11.5$ and $df_2 = 34.5$; $P \sim 0.01$). The relatively high W value was mainly due to the significant correlations (Spearman's rank correlation) between shell size and temperature ($r_s = 0.57$; $P < 0.05$) and between temperature and calcium in soil ($r_s = 0.56$; $P < 0.05$). There were no statistically significant correlations between shell size and calcium in soil ($r_s = 0.04$) or calcium in decaying vegetation ($r_s = 0.17$).

Since data from the monitored population did not show any significant correlation between June values (Table 2) and those of the preceding autumn (i.e. October/November) we decided to test the possibility that, through differential survival, the weather conditions during the period when the snails were in dormancy (i.e. November-March) affected the mean shell size in spring. Mean air temperature was used as a crude measure of the conditions prevailing during hibernation and was found to be positively correlated ($P = 0.017$) with mean shell size in June (Fig. 3). However, we found no significant correlations with minimum or maximum temperatures, number of days with frost, or extent of snow cover.

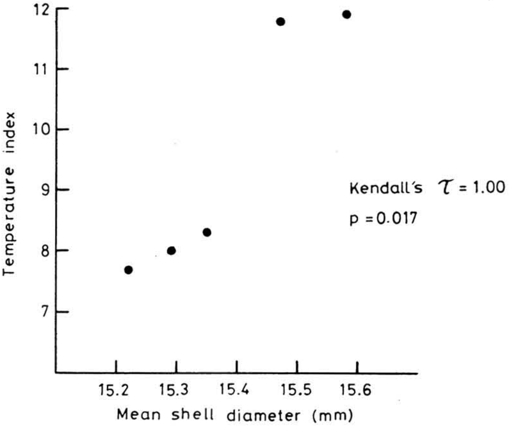

Fig. 3. Relationship between mean shell diameter of adult *C. hortensis* in June and an index of temperature for the preceding winter. The snail samples were collected in June 1973—77 from the population monitored at Vík, southern Iceland, (site 5 in Fig. 1) and the sample sizes are given in Fig. 2. The temperature index is the sum of the mean monthly temperatures during November — March (Veðráttan 1972—77). The correlation was tested by Kendall's ranking. Product moment correlation using individual values ($n = 162$) also showed a significant correlation ($r = 0.20$, $P \sim 0.01$).

5. Discussion

From our field data on the mean adult shell size of *C. hortensis* in Iceland the following conclusions can be drawn:

1) Differences occur in mean shell diameter between areas and even between closely adjacent sites (Table 1), and are relatively consistent from year to year (Table 2).

2) Although all populations are highly polymorphic for shell banding pattern (Owen and Bengtson 1972), the coefficients of variation of shell diameter are small (Table 1).

3) Mean shell diameter may vary seasonally and annually (Figs 2 and 3) at a given site, even though the overall impression is that of relative stability.

4) The variance of the mean may change at any time of year.

The hereditary basis for adult shell size is not known for *C. hortensis* but is probably of the same order as in *C. nemoralis* and *A. arbustorum* (see Introduction). However, Cook (pers. comm.) pointed out to us that his measurements on the heritability of shell size in *C. nemoralis* and *A. arbustorum* were based on between-colony and within-colony crosses and were higher (60 % or more) than the estimates obtained by Wolda on the basis of within-colony crosses of *C. nemoralis* (zero to 40 %). This suggests that the high heritability was due in part to genetic differences between populations.

The effects of environmental factors on adult shell size of *C. nemoralis* have been investigated in the laboratory and under semi-natural conditions, especially by Wolda and Oosterhoff (see Oosterhoff 1977). These studies suggest that much of the variation in the shell size of adults within a population is associated with differences in the growth rate of juveniles influenced by both genetic and environmental factors. Few studies have been made on completely natural populations, though in a population of *C. nemo-*

ralis in Sussex, England, a decrease in mean adult shell diameter was found to be associated with an increase in population density (Williamson et al. 1976). However, selection may act directly on adult *C. nemoralis*, as suggested by laboratory studies carried out by Cook & O'Donald (1971). They found differential mortality among hibernating adults of different sizes and proposed that selection may promote an adjustment of the mean adult shell size to an optimal level in a given site. No comparable studies have been published on *C. hortensis*.

The proximate causes of change in mean adult shell diameter or its variance are: a) recruitment (i.e. juveniles becoming adults), b) migrations, and c) selective mortality among adults. During the growing season when the snails are active all three events may occur simultaneously and it may be difficult or impossible to discriminate between them. During hibernation only selective mortality can cause changes. The population monitored at Vík did not exhibit any significant changes in the mean from one sampling occasion to the next, though during the summers and autums of 1973, 1974, and 1976 some fluctuations occurred. Possibly these slight changes are nothing but sampling errors but it seems equally likely that larger samples would have enabled us to demonstrate significant changes in the mean. Cohorts of large juveniles (subadults) enter the adult cohort of the population in "bursts" and the small fluctuations in mean value coincided with periods of high recruitment rate. As for *C. nemoralis*, it appears highly likely that the growth rate of juvenile *C. hortensis* varies considerably, although we cannot provide any data. Bursts of recruitment may also explain some of the observed changes in variance. In five instances statistically significant ($P < 0.05$) changes in variance occurred: four times in summer and autumn and once during winter. On three occasions (autumns of 1973 and 1974 and summer of 1977) the variance increased, whereas in summer 1974 it decreased. The decrease in the latter part of the summer 1974 may possibly have been associated with the unusually dry conditions, which may, for instance, have inhibited recruitment or caused selective mortality among adults. Normally air humidity in the study area is high (Veðráttan 1972—77). The changes of the variance values did not appear to be correlated with any changes in population density (unpubl. data).

During hibernation no significant changes of the mean occurred, though in winter 1973/74 the variance decreased significantly ($P < 0.05$) and the same tendency was found in 1974/75 ($0.01 > P > 0.05$) which suggests stabilizing selection. The mortality among adults is low during dormancy and only a few empty shells were to be found in spring. Some of them were intact but most had been gnawed by the long-tailed field-mouse *Apodemus sylvaticus* (L.), which is known to prey on hibernating *Cepaea* in the study area (Owen & Bengtson 1972). However, there is no evidence that rodent predation is selective with respect to shell size (or colour phenotype). In view of the observed correlation between mean winter temperature and mean shell diameter in spring ($P = 0.017$) presented in Fig. 3, it seems more likely that climatic factors are involved. Biologically the mean temperature is often not a very meaningful variable and the lack of correlations between shell diameter and extreme winter temperatures, days with frost or the extent of the snow cover is intriguing. The hibernating snails are buried in the soil or in the dense moss and are presumably fairly well protected against short spells of extreme conditions, and possibly the mean temperature better reflects the overall conditions during dormancy.

Climatic factors seem also to be involved in the differences between sites. The significant association between mean shell size, mean minimum temperature, and calcium content of the soil, and of decaying vegetation around Vík in June 1977 ($P \sim 0.01$) was chiefly due to correlations between shell size and temperature and between soil calcium and temperature (both $P < 0.05$). Differences in temperature between sites may lead to differences in the growth rate of juveniles (Oosterhoff 1977) and so possibly affect adult shell diameter. No close correlations were found between shell diameter and calcium either in soil or in decaying vegetation although at first sight the high calcium content of the vegetation at site VI at Drangshlið appeared to coincide with an occurrence of large-sized snails. The climate at Drangshlið is probably favourable and warmer than around Vík, though hardly dissimilar enough to explain the differences in the shell diameter of the snails. One interesting pattern emerges from the Drangshlið data; the mean diameters of snails from sites facing roughly east tended to be smaller than those from sites facing south (Table 1, Fig. 1). In discussing the pattern of morph frequencies in the same area we have argued that south-facing cliffs may provide warmer and more stable temperature conditions than those facing east (Bengtson et al. 1979). This should also hold true for the Vík area, although no similar trend in mean shell diameter could be detected. However, if the high heritability of shell size reported for helicid snails (see above) is due partly to between-colony crosses and genetic differences between populations, the correlations between shell size and environmental factors found within colonies (see e.g. Oosterhoff 1977) may not apply to comparisons between colonies and accordingly large-shelled populations will not necessarily consist of fast-growing individuals (Cook, pers. comm).

Thus, our field data lead us to suggest that spatial and temporal variation in the mean shell diameter of adult *C. hortensis* is governed to some extent by differences in temperature. Variation during the growing season may be due largely to genetic and environmental factors acting on the growth rate of juveniles and on recruitment (Wolda 1972, Oosterhoff 1977). During the winter, when the snails are dormant, selective mortality may affect the mean and reduce the variance, as suggested by the experimental results given by Cook & O'Donald (1971) for *C. nemoralis*. It seems that during relatively warm winters individuals with large shell diameters are at a selective advantage and during colder winters smaller individuals have an advantage (Fig. 3). In the absence of more detailed information on the mechanisms involved, we have to contend with the rather vague term climatic selection. Even small differences in shell diameter imply relatively large differences in body-size/weight (Williamson 1976) and may have profound effects on the physiological responses to environmental conditions such as temperature. The populations of *C. hortensis* in Iceland are geographically peripheral and may therefore be more exposed to environmental selection than many other populations of the species. The maritime climate of southern Iceland implies that seasonal and annual fluctuations in weather conditions are relatively small, which may to some extent explain the apparent stability of mean shell size (Table 2) and the low variability within each of the sites (Table 1).

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