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Variation in growth rate as an ecological factor in the landsnail *Cepaea nemoralis* (L.)

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growing snails of these classes remained juvenile until the next year. For natural populations a positive relation between the increase of the number of adults and the growth rate was shown in chapter 2.

8.4.5. *Adult life span*

In the laboratory at 19°C faster growing snails tended to have a longer adult life span. Not much is known about the age adult *Cepaea* can reach. In the snail-garden (WOLDA, 1973) some snails reached at least the age of 4 years. In natural populations SCHNETTER (1950) recovered adult snails up to 8 years old. In the laboratory (COMFORT, 1957) *Cepaea* has been found to reach the age of 7 years; in our own experiments *Cepaeas* survived maximal 1.8 years as adults.

In the snail-garden the chance of adult snails to survive depended on adult age; the older they were the smaller this chance became. This is, among others, caused by the thrushes selecting on age, and possibly also due to calcium deficiency (WOLDA, 1972). However, this influence of age on survival varied between different populations and between different periods. The growth rate also varied between the different periods and the different populations. My laboratory experiments showed that adults which had grown faster survived longer than slow growers. Therefore an influence of the growth rate on the life expectancy of adult snails seems possible.

As a consequence of the difference in life expectancy between rapid and slow growers the time for reproduction of the former is longer than that of the latter.

9. GENERAL SUMMARY AND DISCUSSION

In two field populations of *Cepaea nemoralis* and under laboratory conditions a study was undertaken of the variation in growth rate and its causation, with the aim of understanding the importance of this variation with respect to changes in numbers and genetical composition in populations of this polymorphic landsnail.

Growth was determined by measuring the increase of shell size. Studies of individual growth curves from hatching till adulthood (chapter 2) showed that the snails first grow at a relatively fast constant rate and later switch to an also constant slower rate; consequently an inflexion point occurs in the growth curve. This feature complicates the comparison of absolute and relative growth rates between samples of snails: comparison is only justified between size classes of snails which are all below or above this inflexion point, or of snails which were of the same size at the beginning of the growth period.

The variation in growth rate under natural conditions was studied (chapter 2) in Haren (plot 8) and in Breekenpolder, in 1969 and 1970. The variation was large in both populations: in 1969 for instance, among snails measuring 3.0–3.9 mm D^1 at the beginning of the growing season the slowest grower increased in the course of the season to 60% of the size of the fastest one. The mean relative growth rate was different between the two populations and the two years. In 1969 the growth rate in BP was about 20% faster than in HA, while in HA the mean relative growth rate was 10% faster in 1970 than in 1969.

Adult size also varied within and between both populations (chapter 2): in 1969 in the HA-population between 16.0 and 23.0 mm and in the same year in the BP-population between 18.0 and 25.0 mm D^0 . The mean adult size in BP exceeded that in HA, and was for both populations in 1970 larger than in 1969.

The time between hatching and becoming adult varied in both populations from one to three years (chapter 2). In BP, however, this period was on the average shorter; in BP a higher percentage of juveniles reached adulthood within one year and of snails of equal size in an equal period more (about 20%) individuals reached adulthood in BP than in HA.

To understand the causation of the variations in growth rate and adult size the influence of environmental (chapters 3 and 5) and of endogenous factors (chapter 8) was studied.

Investigations on the influence of environmental factors on growth rate and adult size led to the following conclusions:

1. Temperature. In the laboratory as well as in the experimental conditions outside, growth rate was correlated with average daily temperature. The maximum growth rate was likely to be reached around 20°C, below 10°C growth came to a stop.
2. Humidity. Experiments in the laboratory and in semi-natural conditions outside point to an optimum relation between growth and humidity. During a drought growth was discontinued and growth was also inhibited under extraordinary high humidity conditions. After a prolonged drought growth showed a "catch-up effect".
3. Light. Growth was found to be inhibited when the light was strongly reduced under laboratory and semi-natural conditions.
4. Calcium. In laboratory experiments calcium was shown to have a positive influence on growth rate, adult size and the thickness of adult shells. If no calcium was present in the environment cannibalism occurred.
5. Population density. Under laboratory as well as under semi-natural conditions, with *ad libitum* food, a negative relation was found between the density at which juveniles grew up and their growth rate

and adult size. A positive relation existed between density and the time between hatching and adulthood. During the entire juvenile period the snails were found to be sensitive to density. No "catch-up effect" in growth rate during a period of relatively low density followed a period of reduced growth at a high density.

The mechanism (see 4.3.2.) through which density exerts a negative influence on growth rate and adult size certainly involves an effect of the mucus secreted by the crawling snails. Although alternative interpretations are not excluded (see p. 66 and Fig. 40) I prefer to think of a direct influence of the mucus, possibly by a toxic effect on metabolic processes. The influence of density on adult size is likely to be caused via the factor growth rate.

Two of the above mentioned factors can account for the differences found in growth rate and adult size (which are correlated with each other, see chapters 2 and 8) between both years. During the most important growth months, May and June, the average daily temperature was more than 1° centigrade higher in 1970 than in 1969, and the density of juveniles was in both populations lower in 1970 than in 1969. The fast average growth rate in BP, in comparison with HA, may have been caused by the density in BP being about 1/3 of that in HA.

The influence of endogenous factors was studied by measuring growth rate and adult size in snails reared in the laboratory for successive generations.

These laboratory experiments revealed a positive relation between growth rate and adult size in the parents and the average value of these characteristics in their progeny. This must be due to genetic factors and/or to other parental influences on the quality of the eggs. The heritability (FALCONER, 1960) was 0.48 for growth rate and 0.58 for adult size.

However, the differences found in growth rate between the two populations in both years could not be attributed to genetic differences.

No influence was found of the genes responsible for colour and band morphs on the variation in growth rate and adult size (chapter 2).

For the assessment of the importance of the variation in growth rate and adult size for the dynamics of the population it is necessary to consider the capacity to survive and to reproduce, and the tendency to migrate.

1. Survival. Our experiments on rearing juveniles in the laboratory at 19°C (chapter 8) and, outside, during winterconditions (chapter 6) have both shown a lower survival rate in relative slow compared with relative fast growing snails. Moreover, fast growers were found to have a longer life expectancy as adult and consequently more time for

reproduction. They also produced juveniles with a lower mortality (chapter 8).

Under humid conditions in the laboratory at 19°C and *ad libitum* food smaller adults had a greater survival rate (chapter 8). We did not succeed in collecting data on the relation between mortality and size of the adults during winter. COOK & O'DONALD (1971) found in the field during a mild winter, and SEELEN (unpubl.) in experiments in the laboratory under dry conditions at 15°C and without food, a higher survival rate in bigger than in smaller adults. However, during a dry summer in presence of food a greater survival rate in small adults is possible (MACHIN, 1967).

2. Reproduction. Relatively fast grown adults and relatively big adults were found to lay earlier, more frequently and to produce larger clutches with a greater mean egg weight, and with a better hatching success. The juveniles produced, were on the average bigger (chapter 8). Moreover, in the laboratory (chapter 8) and under natural conditions (chapter 2) a positive relation was found between growth rate and rate at which the snails become adult, which means that in fast growers the time to produce another generation is shorter.

3. Tendency to migrate. In the field (chapter 7) as well as in the laboratory (chapter 4) fast growers showed a higher tendency to migrate. Correspondingly, data collected by WOLDA (1963) show more migration behaviour in larger than in smaller adults.

The influence of population density on several other variables was studied. Density was not found to influence shell weight, but higher densities did correlate with lower ash-free dry bodyweight, thus with a lower condition of the animal. Moreover, snails grown up at high densities produced relatively small clutches with a relatively low percentage of eggs hatched (chapter 8). In contrast, mean egg weight, development time and mean initial size of the juveniles per clutch were not found to be influenced by the density during the juvenile stage.

WOLDA (1973) is of opinion that juvenile mortality is an important factor determining the number of snails in a population. His data indicate that juvenile mortality is higher at higher densities. My experimental data suggest that this may be due to a decrease of growth rate and condition, either of the juveniles involved or of the parents, or of both.

An increase of the density of adult snails stimulates migration (chapter 4). However, when migration is impossible higher densities inhibit locomotory activity.

A diagrammatical survey of the data collected about the influence of growth rate (and adult size, which depends on it) on the activity, the

reproduction and the mortality of the snails and about the environmental factors influencing growth rate and some other characters of the snails, is given in Fig. 57. The relationships suggest a crucial role of the variation in growth rate in the population dynamics of *Cepaea*

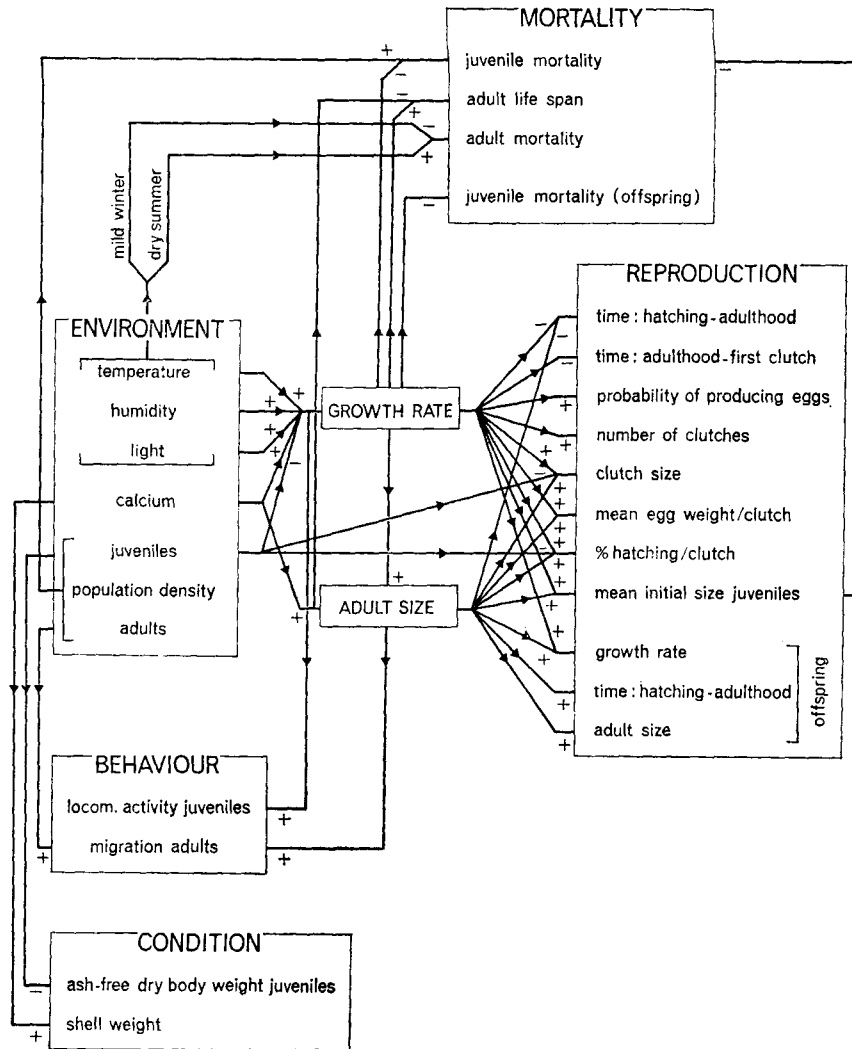


Fig. 57. A diagrammatical survey of the data collected about the influence of growth rate and adult size on activity, reproduction and mortality of *Cepaea nemoralis* and about the influence of environmental factors on growth rate and some other characters of this snail.

nemoralis. A population comprising a considerable number of fast growers will increase faster in numbers than a population of predominantly slow growers. One of slow growers is even likely to decrease; in my experiments very slow growers did not lay at all. Changes in growth rate can be brought about by environmental factors, but more interesting with respect to the changes in numbers of a population is the density-dependency of growth rate and adult size, despite *ad libitum* food. However, population density does not work through growth rate only; it also directly influences the number of snails in the population via the size and hatching percentage of the clutches, the conditions and the survival of the snails, and the migration behaviour. As fast growers have a stronger migration tendency the snails with the largest reproductive capacity will move out first; this will steepen the decline of the population. Provided the environmental factors remain unchanged, the decrease in numbers of the resident population will come to a stop and turn into an increase again when migration is discontinued and the new low density favours an increase of growth rate. With reasonably constant abiotic conditions this mechanism, as represented in fig. 58a, will lead to oscillations of the population density, provided mortality and migration do not act selectively on the frequency in the population of the genes underlying the parameters in the model.

Part of the variation of growth rate and adult size is genetically determined, but selection will sometimes favour faster and sometimes slower growers (chapters 6, 7 and 8). Of considerable importance for maintaining the gene frequency is the great plasticity of the growth rate of a particular genotype in response to abiotic factors. Favourable circumstances may turn a genotypic slow grower into a relatively fast one with all the advantageous effects on mortality and reproduction, and thus for the increase of the number of these animals in the population. A heterogeneous environment may therefore promote the maintenance of an existing gene frequency. Further new genetic variability can occur through selective immigration of relative fast growers.

In this conception the periodical changes in the growth rate of a *Cepaea* population depend on phenotypical changes rather than on genotypical ones. In my opinion in such populations no periodical genetic selection for some character (such as growth rate) will take place, such as assumed by CHITTY (1960) in his hypothesis on the causation of changes in numbers of vole populations. In his model (Fig. 58b) CHITTY postulates periodical changes in the selection for aggressive behaviour.

CHRISTIAN (1950) and WELLINGTON (1960, 1965) in their studies of periodical changes in the population density of mice and of the moth

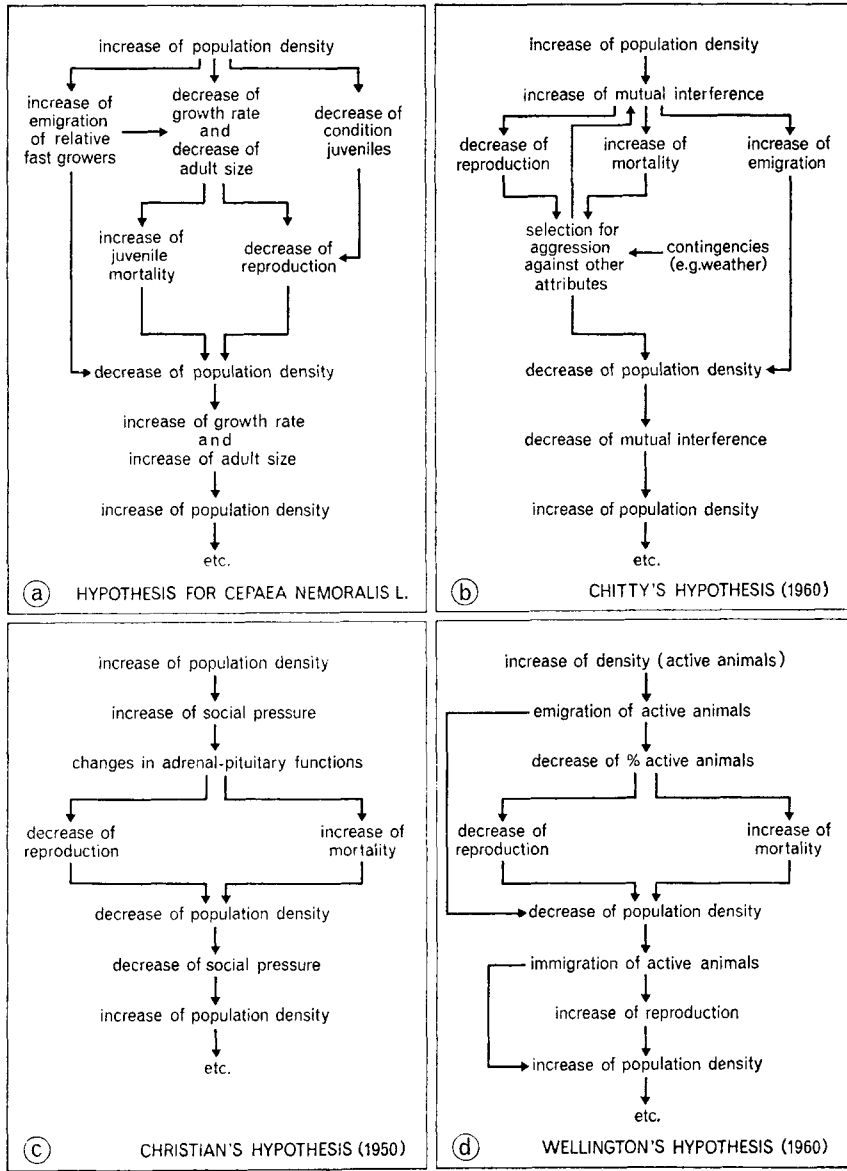


Fig. 58. Four different hypotheses relating the changes in numbers of individuals in a population to changes in composition of the population with regard to ecologically important characteristics.

Malacosoma pluviale, respectively, also postulate changes in phenotypical characters as causes. CHRISTIAN's model (Fig. 58c) assumes changes in adrenal-pituitary functions and WELLINGTON's model (Fig. 58d) changes in activity of the animals.

All four hypotheses have in common that a relation is assumed between the change in number of a population and the mean value of an ecologically important character of the individual. In the models of CHITTY and CHRISTIAN the changes in the mean value of such characters are, like in my *Cepaea* model, thought to be brought about by changes in population density. The change in mean activity in a *Malacosoma* population is caused by a migration tendency which is not dependent on density.

A density dependent effect on growth rate has also been found in *Bupalus piniarius* (GRUYS, 1970). However, the effect turned out to be less important for determining the fluctuations in numbers than other factors, as for instance density dependent migration. A density dependent effect on reproduction was found in the Great Tit *Parus major* (KLUYVER, 1951), but this effect was also less important than the density dependent juvenile mortality and migration (KLUYVER, 1971; DHONDT, 1971).

A determination of the numbers in populations through growth rate and adult size, like I think to have found in *Cepaea nemoralis*, is remarkable. The results of this study amply provide arguments for increasing our attention to the importance of growth rate in the control of population numbers of other species and of other taxonomic groups. This mechanism seems only possible in species where age and size are not narrowly fixed by important selective factors. Such factors could be related to the amount of locomotion and, in general to the extent of the repertoire of activities, which are proverbially limited in snails.

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