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Volume: 48 **Issue:** 3
Month/Year: 1982 **Pages:** * 257-265 *

Article Author: Malacological Society of London Dan, N., Bailey, S.E.R.

Article Title: Growth, mortality and feeding rates of the snail Helix aspersa at different population densities in the laboratory and the depression of activity of

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J. moll. Stud. (1982), **48**, 257-265

GROWTH, MORTALITY, AND FEEDING RATES OF THE SNAIL *HELIX ASPERSA* AT DIFFERENT POPULATION DENSITIES IN THE LABORATORY, AND THE DEPRESSION OF ACTIVITY OF HELICID SNAILS BY OTHER INDIVIDUALS, OR THEIR MUCUS

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ABSTRACT

When reared at high densities, young *Helix aspersa* show less shell growth, even if waste products are removed. They also feed less, and show increased mortality. It is suggested that these effects are linked to reduced activity. Juveniles show reduced activity in the presence of adults or their mucus. Mucus of adult *Cepaea nemoralis* also depresses the activity of both adult and young *Helix* and *Cepaea*.

In many animals the effects of density on growth, mortality, and reproduction are known to be adverse. Often, these adverse effects are produced by an interaction with external factors, particularly competition for food. However, specific growth inhibitors are known, and behavioural interactions also control development, although their role as density-dependent regulators is not so well established.

The effects of population density on freshwater snails has received a considerable amount of attention, particularly from van der Steen and co-workers (see van der Steen, 1977), and Thomas, Goldsworthy, & Benjamin (1975) have demonstrated enhancement of growth in a medium in which other snails have been feeding, although growth is inhibited when the density of feeding snails conditioning the medium is high. Recently, the role of chemicals of a pheromonal nature which affect snail behaviour has been looked at in land snails (e.g. Chase, Pryer, Baker, & Madison, 1978).

The present study establishes a density effect on growth rate and feeding rate in juvenile land snails *Helix aspersa* Müller. Oosterhoff in 1977 proposed that mucus secreted by snails was involved in the regulation of growth by population density in *Cepaea nemoralis*, and Cameron & Carter (1979) showed that activity of *Cepaea* and possibly *Helix* were depressed at high densities and in mucus-pretreated environments. An attempt has been made to discover the causal mechanisms by which these effects operate by investigating the effect of mucus on activity of conspecific snails and other helicids.

MATERIALS AND METHODS

Effects of density on growth and mortality in outdoor cages.

Groups of 10, 40, or 100 snails of all sizes greater than 9.5 mm shell height were placed in three wooden boxes measuring 45.7 × 45.7 × 15.2 cm. Each box was half filled with soil and stones, and covered with a layer of plastic mesh (3 mesh/cm) and netting (9 mesh/cm). Drainage holes were drilled in the base and the boxes placed out of doors for 7 months from November to June. Every few days, cabbage leaves were supplied *ad libitum* at several points in each box. Fifteen adult snails were included, 1 at low, 4 at medium, and 10 at high density. The size range of the other snails in each box was arrived at by first arranging the remaining 135 snails by shell height from smallest to largest. Then, of the 15 smallest animals, 10 chosen at random were

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placed in the high density box, four in the medium density box, and one in the low density box. The procedure was repeated for the next 15 snails, and so on up to the largest snails.

Each snail was numbered, and the edge of the shell marked with red nail varnish. At the end of the experiment, shell growth was measured by cutting away new growth and weighing this and the original shell separately following Herzberg & Herzberg's method (1960). Each month, shell height was measured, and the animals replaced on the surface of the soil. Dead animals were replaced by live animals of similar size, but growth measurements are based only on those original members of each group which survived.

Effects of density and space on growth and mortality in indoor cages

Three groups of 50 juvenile snails between 8.9 and 20.0 mm in shell height were reared in cages of different sizes for 23 months. The snails were numbered and their height each month recorded. Dead snails were replaced by live snails of similar size, but calculations of growth are based on original animals which survived to the time of measurement, and had not become adult.

The 3 cages had floors covered with soil, humus, and pieces of chalk, and wooden tops. The sides and backs were of blue polythene sheet, and the sloping fronts were covered with fine netting partially covered by clear polythene sheet to reduce evaporation. The floor size of the small cage was 45.5 × 42 cm, that of the middle-sized cage 45.5 × 81 cm, and that of the large cage 61.5 × 123 cm, giving floor surface area ratios of approximately 1 : 2 : 4. The combined area of all surfaces over which snails could crawl, namely the floor, sides, back, and top, was 8 460 cm^2 in the small cage. To retain area ratios of approximately 1 : 2 : 4 between the 3 cages for these combined surfaces, the medium and large cages were divided by polythene partitions pierced to allow movement between adjacent compartments.

The cages were kept in a laboratory at room temperatures varying between 15.0°C and 32.5°C. Water was sprayed on to the soil when necessary, and food was provided *ad libitum* at several points in each compartment.

Effect of density on growth in containers cleaned at frequent intervals

Three groups of 2 snails, 3 groups of 4 snails, and 3 groups of 10 snails, all juvenile *Helix aspersa* between 10.5 and 22.8 mm shell height, were kept in nine transparant boxes measuring 12 × 7.5 × 5.5 cm. The floors were lined with moist tissue paper and small pieces of chalk were added. The boxes were subject to daily outdoor temperature fluctuations and daylight, but were shielded from direct sunlight and rain. At least twice each day, mucus and faeces were removed and the animals were provided with fresh cabbage and tissue paper. The experiment lasted 4 months, and shell height was measured at monthly intervals.

Effect of density on food intake of juvenile snails

Two, 4, or 10 juvenile snails of similar size (20.0 to 22.0 mm height) were put into 3 containers measuring 12.0 × 7.5 × 5.5 cm. The floors were lined with moist tissue paper. Only animals which were active and feeding regularly were used. Excess amounts of lettuce of known weight were given. After 24 h at room temperature, the remaining lettuce was removed, cleaned, and weighed to provide the measure of food intake. Under these conditions, very little tissue paper was eaten, and this was ignored. The experiment was repeated 12 times using different animals each time.

Effect of mucus or the presence of other individuals on activity

The following tests were made at night in the late spring or early summer, during the peak months of seasonal activity, on 4 species of helicid snail collected from the Great Orme, Llandudno, N. Wales. The animals were kept together without food or water for 4-10 days prior to use in boxes separated into species. On the night before the test, food and water were provided and the animals used were those which were known to have been active on the previous night.

(a) Five adult *Helix aspersa*, together with adequate food, were placed in a transparent plastic container 12 × 7.5 × 5.5 cm with wet tissue paper on the floor. After 24 h, the animals were removed and a single test snail of the same or a different species was introduced into the

mucus laden container. The test animal was observed by torchlight once every hour for 6 h starting at nine p.m., 3 h after it was introduced. The animal was scored as active if it was moving or feeding, or, if immobile, its foot and tentacles were fully everted.

Twenty replicates were run for each of the following 6 types of test snail: adult and juvenile *Helix aspersa* Müller, adult and juvenile *Cepaea nemoralis* (L.), adult *Trichia striolata* (C. Pfeiffer), and adult *Candidula intersecta* (Poiret) (= *Helicella caperata* (Montagu)).

(b) The same procedures were repeated using 10 *Cepaea nemoralis* adults as the source of mucus.

(c) Procedures (a) and (b) were repeated, except that the animals used to provide mucus were not removed before each test animal was added.

(d) Twenty animals of each of the 6 test types were placed in individual clean containers, and their activity watched as described in (a). These animals formed the control group used to give a baseline level of activity.

RESULTS

Effects of density on growth and mortality in outdoor cages

The experiment was carried out between November and the following June. The results are shown in Table 1. All animals at low density survived, but approximately one third of those at medium and high density died. Most mortalities occurred among individuals which failed to burrow into the soil after they had been weighed in the preceding month, but there was no significant difference in survival of animals of different sizes. Records of shell height show that considerable growth occurred only in the low and medium density boxes in the last month, after the end of hibernation. Nonetheless, measurements of the increment in shell weight over the seven months show that growth is greatest at low density and least at high density. Differences in weight increments are significant only between medium and high density (t-test, $p<0.05$) and low and high density, not between low and medium densities.

Effects of density and space on growth and mortality in indoor cages

In the indoor cages, the mean monthly mortalities, including deaths of replacement individuals, are significantly greater in the small cage (5.09 ± 3.06) than in the medium one (2.87 ± 2.36) (t-test, $p = 0.005$), or the large one (2.26 ± 1.54) ($p < 0.001$), but those in the medium cage are not significantly greater than those in the large one. Growth occurs in all three cages (Fig. 1), and the average growth in shell height calculated by linear regression over the total period was 0.501 mm/month in the small cage, 0.694 mm/month in the medium cage, and 0.616 mm/month in the large cage. However, because few original snails survive the 23 months, the only significant difference is in the linear regression of size between small and medium cages over 23 months ($p < 0.001$). The growth rates over the first twelve months are not significantly different, nor do the final sizes in the small cage differ significantly from those in the other cages. The monthly growth rates of the three groups show no consistency in their fluctuations apart from the decline in growth in the last six months when some animals became adult.

Table 1

Increase in height and weight of shell of juveniles of mixed sizes in three colonies of *Helix aspersa* kept at different population densities out of doors from November to June

Density	Number in box	Survivors after 7 months	Shell height increment per month (mm)		% increase in shell weight over 7 months (± S.E.)
			Nov. to May	May to June	
low	10	10	0.070	2.52	15.00 ± 2.93
medium	40	27	0.073	1.87	9.43 ± 1.55
high	100	69	0.078	0.25	2.13 ± 0.54

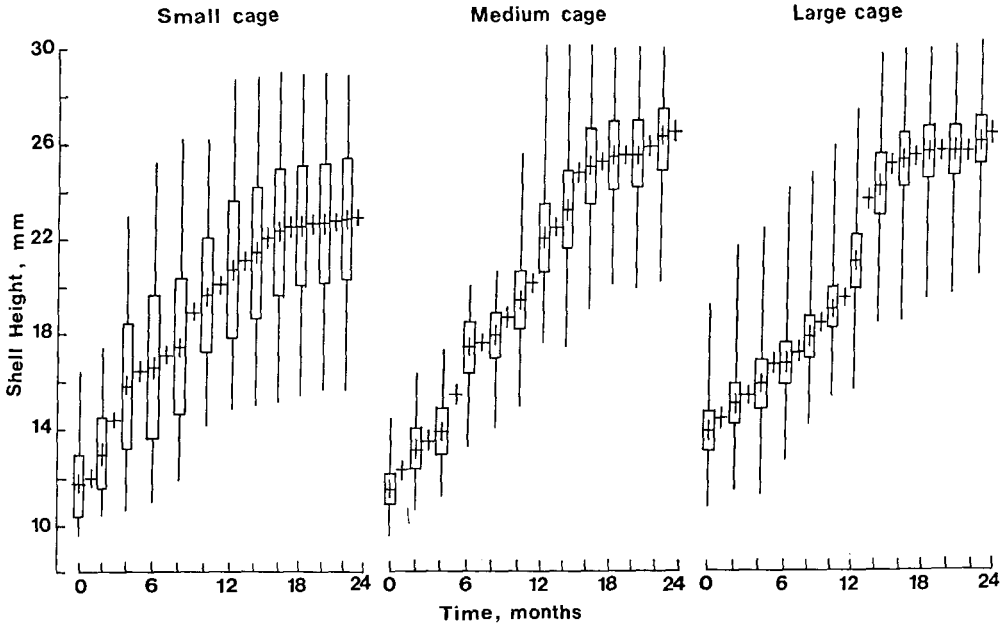

Fig. 1. Growth of *Helix aspersa* indoors over a two-year period, in three cages of different sizes each containing 50 animals. Graphs show the means of shell height of survivors each month, and standard errors and ranges every two months.

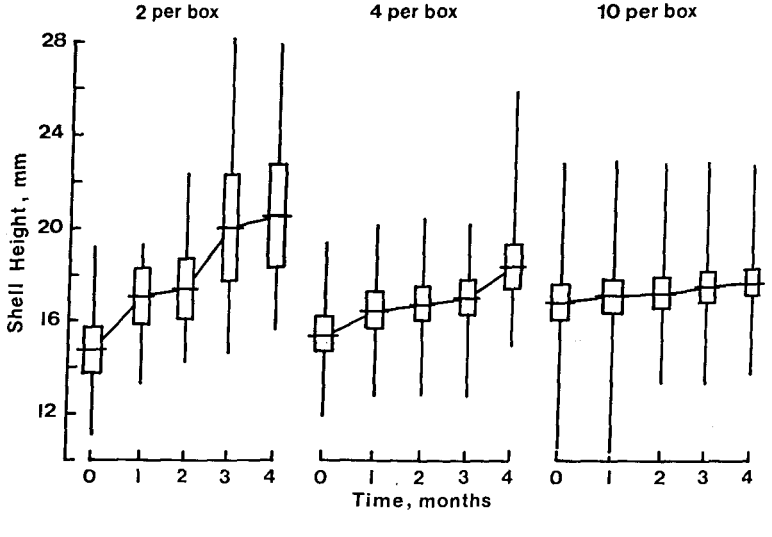

Fig. 2. Growth of *Helix aspersa* over a four-month period in groups of 2, 4, or 10 in a box. Each box was cleaned at least twice each day. Graphs show the means, standard errors, and ranges of shell heights each month, based on the pooled data from three boxes at each density.

Effect of density on growth in containers cleaned at frequent intervals
Although the containers were cleaned several times each day over the four-month period, growth was still slowest in the high density boxes (Fig. 2). From linear regression lines, the average growth rate at low density was 1.44 mm/month, at medium density 0.65 mm/month, and at high density 0.20 mm/month. Only the growth rates at low and high density are significantly different ($p < 0.002$). Of the six animals reared at low density and the twelve reared at medium density, all survived: of the thirty animals reared at high density, twenty two survived.

Effect of density on food intake of juvenile snails
The amount of food consumed by each group is shown in Table 2. From t-test, it is found that there is a significant difference in the food consumed between groups of 2 and 4 snails ($p < 0.002$) and between groups of 4 and 10 snails ($p < 0.01$). It is clear that increase in density reduces the mean amount of food taken by individuals, although food was present in excess.

Table 2
Amounts of food consumed (g wet weight/animal/day) by juvenile *Helix aspersa* in a single 24 h period, when kept in small boxes in groups of different sizes

Replicate	groups of 2	groups of 4	groups of 10
1	0.74	0.31	0.25
2	0.57	0.45	0.30
3	1.10	0.36	0.34
4	0.74	0.32	0.37
5	0.45	0.34	0.29
6	0.68	0.50	0.25
7	1.00	0.48	0.30
8	0.81	0.41	0.32
9	1.47	0.57	0.31
10	0.68	0.70	0.54
11	0.87	0.78	0.49
12	1.23	0.85	0.30
mean	0.86	0.51	0.34
standard error	0.09	0.06	0.03

Effect of mucus or the presence of other individuals on activity
Table 3 shows the total scores of activity of 4 species of test snail in boxes previously occupied by 5 adult *Helix aspersa* or 10 adult *Cepaea nemoralis*, and compares these scores with those of control animals in mucus free containers. Each activity score is the total of 6 observations made on one night on each of 20 snails in individual containers: the maximum activity score possible is thus 120. The design of the experiments makes a statistical analysis by 2x2-frequency chi-squared tests unsuitable, and therefore the mean activities of each test and control group have been compared by t-test with 38 degrees of freedom. The probabilities shown are those of significant difference: probabilities that the levels of activity are lower in the test groups than in the controls are half those shown.

It was found that in containers which had become laden with mucus of adult *Helix aspersa*, the activities of juvenile *Helix aspersa* and *Cepaea nemoralis*, and of adult *Trichia striolata* were inhibited, whereas those of adult *H. aspersa*, *C. nemoralis*, and *Candidula intersecta* were not. In containers mucus laden by adult *Cepaea nemoralis*, the activities of all types of test snail, except *Candidula intersecta*, were inhibited.

When the same types of test snail were introduced into boxes still containing other snails, the activities of the introduced animals were highly inhibited by comparison with the control groups (Table 4). Each group showed more time inactive than active, although juvenile *Cepaea* were less inhibited by other snails than by mucus of adult *Cepaea* alone.

Table 3
The activity of test snails isolated in boxes laden with mucus from adult *Helix* or *Cepaea*, compared to activity when isolated in clean containers

Test Species	Tests in isolation	Tests in presence of mucus of adult *Helix aspersa*			Tests in presence of mucus of adult *Cepaea nemoralis*		
	Total activity	Total activity	t	Probability	Total activity	t	Probability
adult *Helix aspersa*	85	68	1.96	N.S.	63	2.50	<0.02
juvenile *Helix aspersa*	113	63	2.84	<0.01	64	5.83	<0.001
adult *Cepaea nemoralis*	80	61	1.98	N.S.	52	3.04	<0.01
juvenile *Cepaea nemoralis*	71	9	8.61	<0.001	9	8.86	<0.001
adult *Trichia striolata*	99	66	2.89	<0.01	53	3.77	<0.001
adult *Candidula intersecta*	94	81	1.71	N.S.	78	1.45	N.S.

Table 4
The activity of test snails in boxes containing adult *Helix* or *Cepaea*, compared to activity in isolation in clean boxes

Test Species	Tests in isolation	Tests in presence of five adult *Helix aspersa*			Tests in presence of ten adult *Cepaea nemoralis*		
	Total activity	Total activity	t	Probability	Total activity	t	Probability
adult *Helix aspersa*	85	40	9.00	<0.001	40	9.00	<0.001
juvenile *Helix aspersa*	113	28	17.00	<0.001	26	18.91	<0.001
adult *Cepaea nemoralis*	80	36	5.50	<0.001	28	6.36	<0.001
juvenile *Cepaea nemoralis*	71	26	5.23	<0.001	17	2.15	<0.05
adult *Trichia striolata*	99	34	7.39	<0.001	29	8.97	<0.001
adult *Candidula intersecta*	94	36	7.25	<0.001	18	11.18	<0.001

DISCUSSION

The first three experiments have shown that in crowded conditions, *Helix aspersa* juveniles grow more slowly, even if waste products are removed: they possibly mature at a smaller size, and their mortality is increased. The densities used to demonstrate the effects were higher than the overall densities of 1-2.m^{-2} found in the field (Dan, 1978), but the use of communal roosts increases local field densities. In *Cepaea nemoralis*, Williamson, Cameron & Carter (1976) showed a relationship between field density and adult size, and Wolda (1970) and Oosterhoff (1977) have demonstrated a positive relationship between growth rate and adult size. Cameron & Carter (1979) showed that growth rate and activity of juvenile *C. nemoralis* were inversely related to density.

Deaths in outdoor cages over winter occurred predominantly among unburied animals, which were least protected from cold and desiccation. Williamson (1958) suggested that competition for shelter from predators also might limit the overwinter population size of *Helix aspersa*. In the indoor cages too, there may have been competition for suitables sites. However, the numbers of such sites in the three cages may not have been in the same 1 : 2 : 4 ratio as the surface areas: for example, the ratio of the numbers of corners was 1 : 2 : 3. Maintaining an adequate humidity was most difficult in the large cage, and may account for the slower growth in the large cage compared to the medium one.

The effect of density on growth was seen even when waste products were removed, suggesting that these are not a major source of inhibition, contrary to the suggestion of Herzberg (1965). The continuous growth exhibited in Herzberg's experiments was possibly due to the disturbances associated with cleaning, for Bailey (1975) found that daily activity was greatest on the night following cleaning, and declined on subsequent nights.

The reduction in feeding rate at high population density shown by juvenile *Helix aspersa* was also found in *Lymnaea stagnalis* by van der Steen (1977). It is doubtful if feeding rate of land snails is ever limited by food quantity in the field (Boycott, 1934; Williamson *et al.*, 1976), even although food selection occurs in *Helix* (Dan, 1978) and *Cepaea* (Richardson, 1975), so density will not control feeding rate by limiting food supply. Van der Steen, Jager & Tiemersma (1973) suggested that food may be a limiting factor for freshwater snails, even where it is seemingly supplied *ad lib.*, but this limitation arises where the sensory capabilities of the snails and the manner of food distribution makes food finding difficult. However, Grime, Blythe & Thornton (1970) and Farkas & Shorey (1976) have shown that land snails can detect food at a distance, and ample food was spread about the cages so making it readily available to all individuals.

Feeding rate in aquatic snails has been closely correlated with growth rate by Thomas *et al.* (1975), but there is evidence that density also affects growth directly (Oosterhoff, 1977; Mooij-Vogelaar & van der Steen, 1973; van der Steen, 1977). Thomas (1973) rejected the idea of a specific growth-inhibiting pheromone, but several workers on freshwater snails have suggested that a chemical which affects growth is present at high density (Thomas *et al.*, 1975). The idea that mucous tracks may serve roles other than their primary locomotor one, in altering the behaviour of other individuals, is an obvious and attractive one. Oosterhoff (1977) showed that growth and locomotor activity of isolated snails are strongly correlated, and both are suppressed by either a high density of juveniles, or by supplying extra mucus. Cameron & Carter (1979) showed a direct effect of mucus on activity. In Oosterhoff's work, the depression of locomotor activity at high juvenile density was only shown after three months: immediately after their introduction to high density, her snails showed increased activity. She was therefore able to explain the increased emigration seen at high density as the first response to high density, and lowered growth as a response resorted to in a closed system (as did Thomas *et al.*, 1975). Oosterhoff further suggested that growth rate was affected by mucus not only by a link with activity and food consumption, but also directly. In the present study, and that of Carter & Cameron (1979), the presence of mucus from adult snails of the same or a different species often depresses the activity in the hours following its introduction. There was no indication in either study that activity was increased in the presence of mucus.

Oosterhoff considered that the mucus was not depressing activity by acting as a physical barrier, and in the present work, the smallest species used, *Candidula intersecta*, showed no significant depression of activity in either test. It therefore appears that active substances present in the mucus may be operating either indirectly, via sense organs, or directly, as biochemically active toxic substances. It is unlikely that mucus acts after its ingestion with food because preliminary observations on feeding rates in arenas supplied with mucus-contaminated food showed no consistent differences from feeding rates in other arenas, and Oosterhoff obtained no significant difference between growth in dishes with extra mucus supplied on both filter paper and food, and dishes with extra mucus supplied on filter paper alone. Furthermore, the reduction of activity is relatively rapid for an effect gained through ingestion.

As shown in Table 3, the mucus of both *Helix* and *Cepaea* adults inhibits the activity of adults and juveniles, but has more effect on juveniles, the effect of *Helix* mucus being insignificant on adults of three of the species. This suggests that the control is aimed more at juveniles,

and less at adults (including the producers themselves). The later stages of mosquito larvae (Ikeshoji & Mulla, 1970) and tadpoles (Rose, 1960) both produce growth-retarding factors which are most effective on earlier stages, and hence larger animals retard or suppress the growth of smaller ones. In snails, the effect of mucus from juveniles has not been tested, but in the feeding experiments, where only juveniles were used, a depression of food intake occurred at high density, and Oosterhoff also demonstrated an effect of density on juveniles which had not been in contact with adults. It is possible that these effects were due to the mucous tracks of other individuals.

The increased inhibition generally exhibited in the presence of other individuals (Table 4) can be explained in at least two ways. First, the mucus present is much fresher than when the animals are removed before introducing the test animal, and the effectiveness of a particular active substance in the mucus tracks may decay rapidly. Secondly, the inhibition may be increased by direct interaction between individuals. Mechanical stimulation may be adequate, as Lees (1967) demonstrated in aphids, where increased number of contacts caused the production of alate daughters. In this case, the interaction must differ from the type of disturbance caused by cleaning which results in increased activity and growth: Lees could artificially duplicate the effects of mechanical interaction in aphids only by introducing other species of insect. An alternative form of direct interaction may be the production of a special type of mucus in response to stimulation by other snails. It is well known that many slugs produce a special type of mucus when irritated, and the opisthobranch *Navanax* produces an "alarm substance" in its mucus under certain conditions, which causes trail-following conspecifics to break away (Sleeper & Fenical, 1977).

The growth-retarding factors of mosquito larvae and tadpoles showed some action on closely-related species. Cameron & Carter (1979) showed interspecific effects only between two species of *Cepaea*, not between *Cepaea* and *Helix*. Our experiments clearly show interaction between *Helix* and *Cepaea* but the amounts of mucus present in our experiments were probably much greater, and the periods of exposure were longer. Our experiments were also different in that they were conducted at night. From the t values in Table 3, it appears that *Cepaea* mucus has a stronger inhibitory effect than that of *Helix* on all test species, including *Helix*. Ten *Cepaea* were used in place of five *Helix* because of the different foot sizes, but the actual amounts of mucus present are unknown.

ACKNOWLEDGMENTS

We are grateful to Prof. E. R. Trueman for providing the facilities necessary to carry out this research in the Department of Zoology, University of Manchester, and to the University Kebangsaan Malaysia for their financial support to one of us (N.D.) during the period of research.

SUMMARY

1. The shell growth of juvenile *Helix aspersa* is reduced, and mortality increased when they are reared in cages under crowded conditions.
2. Growth rates are lower at high density even when waste materials are removed and food replaced at frequent intervals.
3. Juvenile *Helix aspersa* consumed less food at high density.
4. Locomotor activity of isolated snails in boxes previously laden by mucus of adult *Helix aspersa* is generally lower than that of controls. Adult *Helix aspersa* and *Cepaea nemoralis* are not significantly affected, but juveniles of these species and adult *Trichia striolata* are. In boxes mucus laden by adult *Cepaea nemoralis*, adult and juvenile *Cepaea* and *Helix* show less activity than controls. Adult *Candidula intersecta* show no significant depression of activity.
5. When introduced into boxes containing adult *Helix* or *Cepaea*, all types of helicid snail show considerably less activity than the controls.

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