THE EFFECTS OF DISPERSAL IN LABORATORY POPULATIONS OF THE POND SNAIL, PHYSA GYRINA SAY

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ABSTRACT

THE EFFECTS OF DISPERSAL IN LABORATORY POPULATIONS OF THE POND SNAIL, *PHYSA GYRINA* SAY

By

Judith Sauvé Warner

Aquatic grazers generally feed on the substrate over which they move, so that their ability to detect differences in substrate quality is not unexpected. However, their ability to distinguish quantitative differences in available food and the effects that this ability may have on their populational responses are largely uninvestigated. This study examines the responses of such a grazer, the pond snail *Physa gyrina* Say, under controlled access to quantitative differences in a food substrate. Two replicated populations are compared: the controls, with 15 snails each, were subdivided into three groups restricted to discrete food levels; the experimental populations had unrestricted access to the three food levels. These food levels were discrete patches consisting of 1, 5, and 10 particles of spinach, placed in separate feeding stations.

On the short term, neither the shell growth, survivorship nor the number of eggs produced differed between the unrestricted

and the control populations. However, the unrestricted snails dispersed non-randomly in the experimental populations, their densities increasing with higher numbers of food particles per patch. In addition, the feeding frequencies of these unrestricted snails were more highly correlated with the number of food particles available at the different patches.

Although both populations had similar survivorships, the snails in the unrestricted populations ate and damaged less of their food each day. As a result, the experimental populations realized a greater carrying capacity than did the restricted population.

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By

Judith Sauvé Warner

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I've learned a lot from my association with these people and research groups, especially from the Ecology Group at Michigan State University. Most importantly, I've learned that each of us perceives our own reality.

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INTRODUCTION

A major factor in the dynamics of natural populations and the regulation of animal numbers is the dispersal of individuals over the resource heterogeneities of their environment (Dayton 1971; Krebs et al. 1969; Meyers and Krebs 1971). This dispersal is an adaptive response especially in spatially heterogeneous environments where there are real or apparent differences in the animals' limiting resources (Spright 1974). Yet the specific ecological constraints effecting this dispersal activity can not always be inferred from the final distribution patterns alone (Connell 1963). For example, behavioral interactions such as competition can result in both random and non-random dispersion patterns (Pielou 1969); while both under- and overcrowding can result from dispersal in populations whose habitats vary in carrying capacities (Gadgil 1971). Still, dispersal or the lack of it has been shown important in laboratory systems of predator-prey interactions (Huffaker 1958; Matsomoto and Huffaker 1973) and competitive interactions (Cotter 1974; Ghent 1966; Lomnicki and Slobodkin 1966; White and Huffaker 1969).

Whether for predator-prey systems or for competitors, the predictive models for consumer strategies further underscore the importance of dispersal in community ecology and population dynamics (MacArthur 1972; Pianka 1974). This is because dispersal involves not only the movement of animals and their distributions, but is also a factor in the resource allocation strategies of animals as consumers. Most of these models argue from the standpoint of food as the allocated resource, with the optimum strategy requiring efficiency in searching, pursuing and/or capturing food particles. But while many predators, including seed predators, have foraging behaviors that are quantifiable in terms of the particle sizes they select (Holling 1966; Janzen 1971; MacArthur 1972), the foraging strategies of herbivores, especially grazers, appear more qualitative as they disperse over an apparent continuum of food resources (McNab 1963). Thus the foraging strategies proposed for herbivores have them spending most of their time searching for food, selecting habitats and foraging as generalists on the quality or palatability of their food substrates (Hairston et al. 1960; Harper 1969; MacArthur 1972). Not only have these models of resource allocation not been extensively tested for grazing species, but little is known about their behavioral and populational responses to quantitative food levels (Harper 1969).

The Experimental System

Here I examine the ability of an aquatic herbivore to distinguish among food patches with different amounts of food in them, and compare the effects of such unrestricted foraging to control populations restricted to fixed food levels. To test these effects, I chose a small aquatic gastropod, *Physa gyrina* Say, and a simple experimental system. *Physa* is a visual, gregarious pond snail with chemoreceptive abilities (Wells 1965); it disperses actively in field populations and can move more than ten cm in five minutes (Clampitt 1970). It can be sensitized to shocks but does not learn to avoid them (Wells and Buckley 1972; Wells and Wells 1971). Still, *Physa* discriminates among species of emergent vegetation (Pip and Stewart 1974; E. Pip, pers. comm.) as it continually grazes the substrate over which it moves.

In general, the foraging strategies of pond snails are relatively unknown, except for their responses to certain qualitative differences in available food (Eisenberg 1966; Townsend 1973). For this reason, I kept the complexity of the experimental systems to a minimum and restricted structural heterogeneity to the presence of glass finger bowls. These bowls served as feeding stations within the larger volume of the population tray. Replicated populations were set up to compare the population responses (reproduction, growth, and survivorship) and the feeding behaviors of Physa as a grazer under controlled access to its food. The experimental or unrestricted populations consisted of snails which were free to disperse among quantitative levels of a single food source (spinach), while the control or restricted populations were subdivided into groups of snails confined to these different food levels.

Two factors determined the length of the experimental run. First, the snails had to have enough time to respond, i.e. days rather than hours. Second, at 20° C, Physa's eggs hatch in 14 days, but reproductive maturity is not reached for another 40 days (Clampitt 1970). However, survivorship for pre-reproductives is very sensitive to culturing conditions (R. M. Eisenberg pers. comm.) and mortality in either adults or pre-reproductives would supply an extraneous food source to the snails which readily feed on any organic material, thus confounding the populational responses compared here. Therefore I collected egg masses daily, did not allow reproductive recruitment into the populations, and terminated the experiment on the 14th day.

Predictions

Studies have shown that the densities of natural populations of pond snails can be regulated through the adjustments of their fecundity, growth, and survivorship around extant food supplies (Eisenberg 1966; 1970). Because these population responses are sensitive to food levels, at the outset two contrasting predictions were made for the populations designed in the present experiment. First, snails restricted to fixed food levels in the control populations might consume more of their food simply because of their restrictions to it. But if higher food consumption occurred, then these populations should have higher egg production, greater growth and/or survivorship. In contrast, all or some of these same population responses should be lower in unrestricted populations whose snails would be expending energy in dispersal and the search for food.

Alternatively, snails dispersing among the different food levels in the experimental populations might more efficiently exploit the different food levels through their abilities to move in and out of the feeding stations. If the unrestricted snails disperse and thus displace intraspecific interference at the food patches by expanding their use of the spatial resources, then their opportunities to feed at productive food levels with less interference might increase. If such feeding resulted in food consumption beyond the energetic demands of dispersal and maintenance, then their populational responses in reproduction, growth and/or survivorship might increase. These same responses should be correspondingly lower in the groups of restricted snails because of the relatively small volumes in which they live and the consequent interference over fixed (and possibly limiting) food levels.

METHODS AND MATERIALS

Each population, replicated five times, consisted of fifteen adult snails in a plastic tray (41 x 46 x 11 cm) with three glass finger bowls serving as their feeding stations. These bowls were 10 cm in diameter, five cm deep and filled with 130 ml of filtered tap water. This water level was two cm below the bowl rims and was an effective barrier to emigration by the pond snails. The food particles, fresh spinach leaves cut into 15 x 15 mm pieces, were about twice as large as the area covered by a single snail; therefore, a snail on such a particle was feeding on a continuum rather than engulfing a single unit of food. In addition to its high food value to pond snails (Eisenberg 1966), fresh spinach does not disintegrate with the boiling required to prevent floatation of the particles.

Each of the three feeding stations in a tray held a different number of spinach particles and designated a food level or patch size: low food = one particle; medium = five; and high = ten particles. In order that the three stations in each tray be about the same distances from its walls and from the 25 watt incandescent light bulb over each tray, I placed them at the corners of an equilateral triangle in the in the center of the tray, about three cm apart. The high food level was to the right, the low to the left and the medium, between and in front of the other two stations. The lights were kept on a 12-hr. light, 12-hr. dark photoperiod, which also helped maintain the water temperatures within narrow limits ($22 \pm 2^{\circ}$ C).

From a laboratory stock culture, I sorted 150 adult <u>Physa</u> (mean length: 8.4 ± 0.1 mm) randomly into three groups for marking. Individually identifying the fifteen snails in each population meant prohibitive bookkeeping, but both the growth and the distributions of subsets within the populations could be followed using three color categories. Therefore I marked snails with one of three different colors of Testors Pla Enamel (The Testor Corp., Rockford, Ill. 71101) and drew five snails from each category to make up a population. The snails of a given color code were arbitrarily assigned to a given food level: yellow to low food; orange to medium; and red to the high food level.

At the beginning of the 14-day experimental run, the trays of the experimental or unrestricted populations were filled with 18 liters of tap water, filtered for visual particulate matter. This water level, about two cm above the bowl rims, permitted the snails to disperse freely among the feeding stations; but because the bowls were not touching, snails had to crawl out of one and onto the tray before entering another. The trays of the control populations were filled with 16 liters of water, about two cm below the bowl rims and so remained as restricted populations, subdivided into groups of five snails at each feeding station.

Two observations were made each day. In the mornings, after about two hours of light and with spinach particles that had been exposed to about 24 hours of feeding activity, the following data were taken: densities at the food levels and in the trays; mortality; feeding densities; the number of food particles eaten, damaged (i.e. with rasped holes) and intact. Egg masses were then collected, fecal material and food particles removed, and fresh food and water supplied. About six hours later, the afternoon observations were made on densities and feeding activity, but generally no feeding damage had occurred by this observation period. *Physa* grazes constantly as it moves over its substrate, but a snail rarely moved immediately from a spinach particle once it was on it, even if another snail also moved onto it too. Therefore, a snail was recorded as feeding only when it was on a spinach particle.

A split-plot experimental design (Appendix A) was used to analyze the response variables (Gill and Hafs 1971; Kirk 1968). All data reported as percentages were transformed to arcsine units for the analyses of variance (Sokal and Rohlf 1969). Frequency data were analyzed using Chi square tests, which are reported as ($X^2_{\alpha[d.f.]}$ (tabular value) $\lessgtr X^2$ (Calculated value)). Where there were significant differences in the response variables over food levels or with time, regression analyses were used to test the trends. Sample size for each mean was N = 65, unless otherwise noted.

To characterize the distribution of snails in the unrestricted populations, I recorded the snails' positions by quadrants. These were visual divisions of the trays; first I used crossed diagonals from the corners, and as a second check, Cartesian coordinates through the center of the trays. Then the distributions of the snails among the different food levels, the tray quadrants, and their frequencies on the walls versus the tray floors were tested for randomness, using t-tests on the variance:mean ratios of densities (Kershaw 1964; Stiteler and Patil 1971).

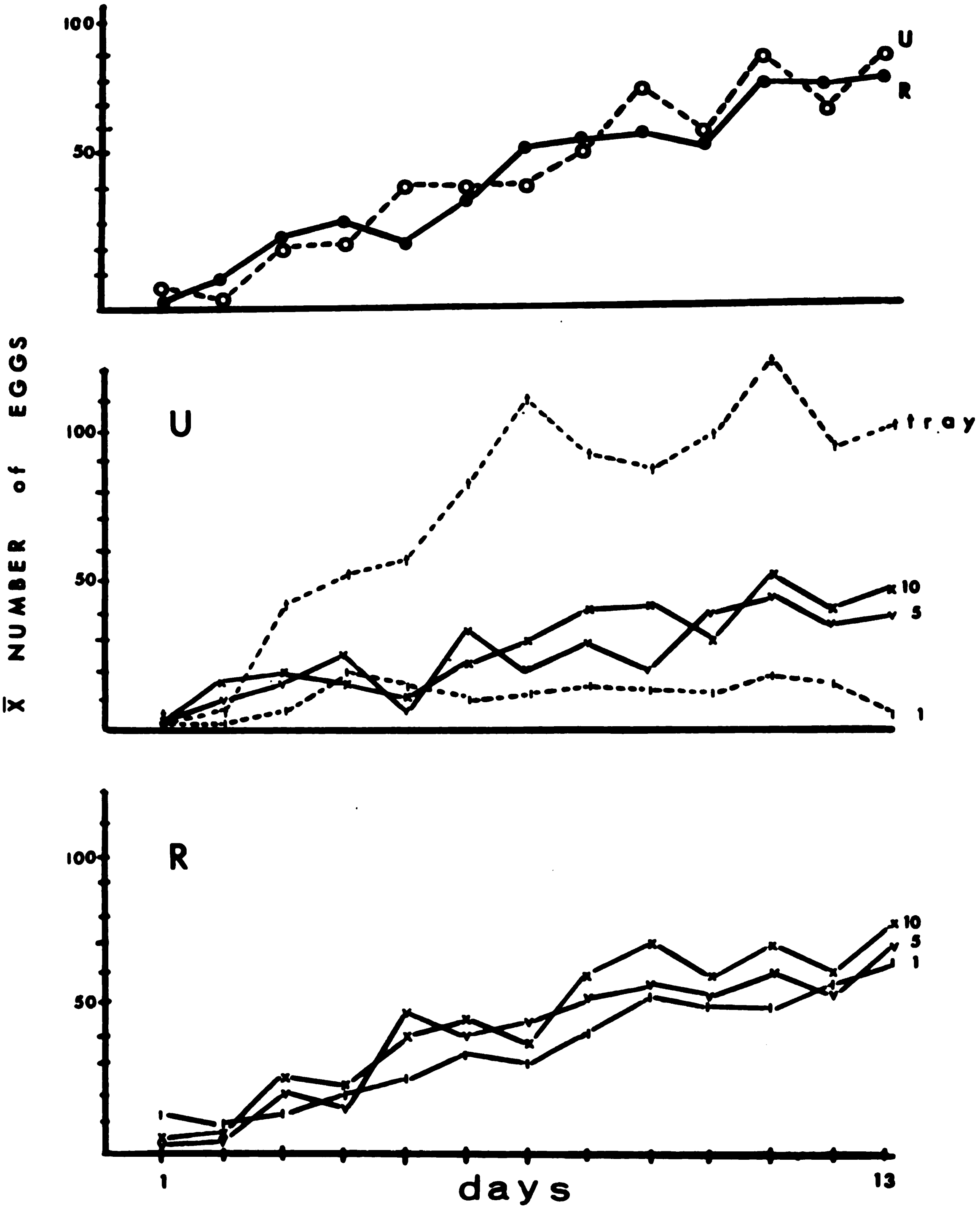
RESULTS

Reproduction

Under laboratory conditions, reproduction in P. gyrina can be affected by culturing conditions and snail densities (Clampitt 1970; van der Schalie and Berry 1973). But although in the present study the experimental populations produced a total of 8% more eggs and egg masses than did the controls, the average number of eggs laid each day (35 ± 3), their clutch size (24 ± 2) and infertility (38 ± 3%) did not differ. Overall, each of these reproductive characteristics were poorly correlated with the food levels provided and with the amounts of food actually eaten or damaged in each population.

Most of the eggs produced in the experimental populations were laid in the trays: but despite the poor correlations between egg production and food levels, the number of eggs laid at each food level differed significantly ($P < 0.005$; Figure 1). All reproduction in the control populations occurred in the feeding stations, and though significantly higher than that at the comparable experimental food levels, the average number of eggs laid did not differ among food levels in the controls ($P < 0.05$; Figure 1).

Figure 1.--Mean number of eggs laid in the experimental (U) and control (R) populations; at each food level (1, 5, 10) and in the trays (t) during the experiment.


100
50
U
R
X̄ NUMBER of EGGS
U
100
50
tray
10
5
1
R
100
50
10
5
1
1
days
13

Over the fourteen day experiment, the egg production in each population increased linearly ($P < 0.005$) but their slopes (production rates) did not differ. Within the experimental population, however, the number of eggs produced at the low food level did not increase over time, while the production rates at the medium and high food levels (though not different) were significantly lower than that in the trays ($P < 0.001$). Therefore, significantly more eggs were laid away from the feeding stations in the unrestricted populations as the experiment progressed. In the control populations, eggs were laid at a signficantly lower rate at the low food level ($P < 0.05$), though this did not reduce the average number of eggs laid there.

Overall, clutch size (eggs/egg mass) did not differ between the two populations. However, larger clutches were laid at two sites: in the experimental populations' trays where there was no food; and at the high food level in the control populations where these larger clutch sizes were highly correlated with food consumption. In contrast, clutch sizes were significantly smaller at the low food level in the experimental populations and were not correlated with food consumption there.

Neither the number nor the percentage of infertile eggs differed between the two populations ($P < 0.001$); but among food levels in both populations, the percent of infertility was significantly different ($P < 0.05$). In both populations, it was highest at the medium food level (44 ± 3%), and lowest at the high food level (19 ± 2% for the experimental populations; 26 ± 2% for the controls).

Growth and Survivorship

Although shell length is considered a reliable index of age in populations of *Physa* and other snails (DeWitt 1955; Pollard 1973), growth in field populations of aquatic snails is affected by food limitations (Eisenberg 1966). Under laboratory conditions, growth is also affected by such culturing variables as the size distributions and densities of the snails; food composition; volume; and conditioning periods (DeWitt 1954b, 1955; Eisenberg 1970; van der Schalie and Davis 1965). Fed ad-libitum amounts of lettuce, *P. gyrina*'s fastest growth is in its first five weeks after hatching and before it reaches sexual maturity at about 45 days and seven mm in length (Clampitt 1970; DeWitt 1954a, pers. comm.).

There was no significant growth in either experimental or control populations (Table 1), but these snails had matured under abundant food conditions in an uncrowded stock culture so that at 8 mm in length, they were of a size category that would be putting energy into reproduction rather than growth. Because they were equally free to disperse among all food levels, there was no reason to expect differential growth in the color categories of snails in

TABLE 1. Growth and survivorship. Mean ± 1 S.E. shell length (mm); and number of snails alive during the experiment.

	Populations		
	Experimental		Control
Length			
overall			
on day 1	8.4 ± 0.06		8.5 ± 0.08
day 14	8.4 ± 0.04		8.6 ± 0.05
color categories		color categories	
on day 14:		restricted to:	
yellow	8.5 ± 0.05	low food (y)	8.3 ± 0.07*
orange	8.3 ± 0.02	medium (o)	8.8 ± 0.02
red	8.6 ± 0.03	high (r)	8.8 ± 0.02
Number alive (on day 6 of expt.)	14.5 ± 1.8		13.6 ± 1.7
Percent surviving to end of experiment	96.6		86.6

*significantly different among food levels ($P < 0.05$).

the experimental populations, and there was none. However, in the control populations, the snails surviving at the low food level were smaller, while the snails at the medium and high food levels were larger than any of the color categories in either population ($P < 0.05$, Table 1). Therefore, snails restricted to the low food level not only did not grow, but apparently only the smaller individuals from the initial size distribution survived there to the end of the experiment. But snails specifically restricted to the higher food levels showed significant growth over the unrestricted populations.

Four snails died in the experimental and ten snails in the control populations, so that the former had a significantly higher percent surviving to the end of the experiment ($P = 0.05$; Table 1). In the control populations, most of the mortality (8 snails) occurred at the low food level, but because most of these snails died after the eleventh day of the experiment, the mean number of snails alive during the experiment did not differ between the two populations.

Dispersal in the Experimental Populations

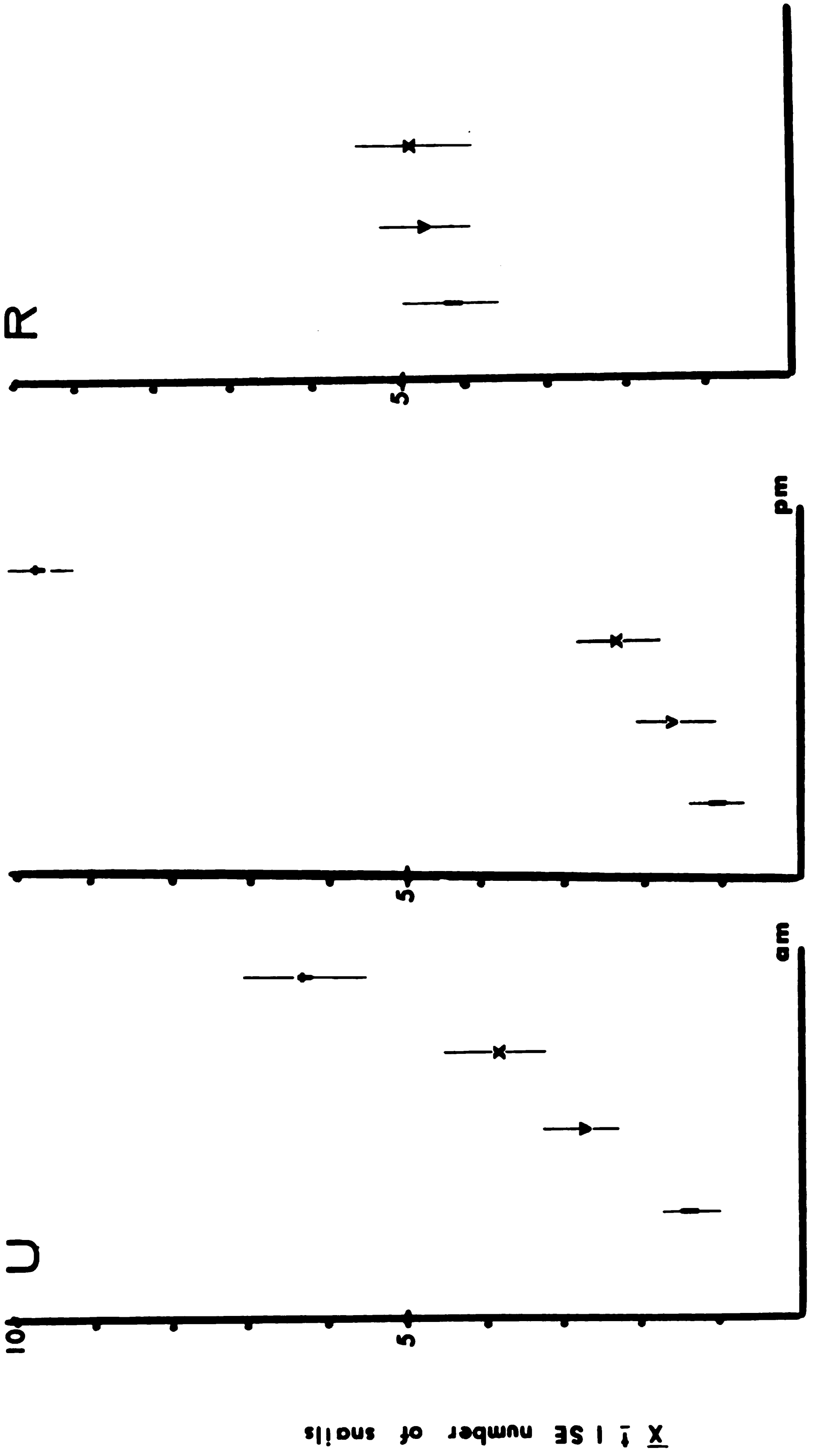
As expected, the control feeding stations were effective barriers to emigration, and only four different snails moved from their stations into the population trays. Therefore mortality alone affected the number of snails in these restricted populations.

However, snails dispersed actively in the experimental populations, and this dispersal determined the snail densities among their food levels.

These unrestricted snails did not favor the feeding stations over the tray quadrants but were equally frequent in the two general areas ($\chi^2_{.05[1]} > 0.07$). Also, they were randomly dispersed among the tray quadrants ($\chi^2_{0.05[3]} > 6.03$), and did not frequent the walls over the floors of the trays ($\chi^2_{0.05[1]} > 2.53$). An obvious orientation to a specific area, say away from or near the overhead light bulb, therefore did not occur.

The unrestricted snails, however, were not randomly distributed among food levels ($\chi^2_{0.05[2]} < 180.3$). That is, their densities differed among food levels ($P = 0.01$; Figure 2) increasing, linearly, with the number of food particles present ($P = 0.05$). In addition, there was a diurnal shift in densities at the feeding stations, which reflects the fact that the snails did not remain in them for long periods and thus were not more frequent in the feeding stations than in the trays. Specifically, at each food level, there were always more snails present in the morning observations than in the afternoons (Figure 2). Significantly though, in each observation period, morning and afternoon, the densities at each food level did not vary significantly over the days of the experiment ($P < 0.05$). Therefore, each day the snails moved in and out of the unrestricted feeding

Figure 2.--Mean ± 1 S.E. number of snails present in the experimental (U) populations in the morning (am) and afternoon (pm) observations. Control (R) observations are averaged over both observations.


R
U
am
pm
10
5
5
5
X̄ ± 1 SE number of snails

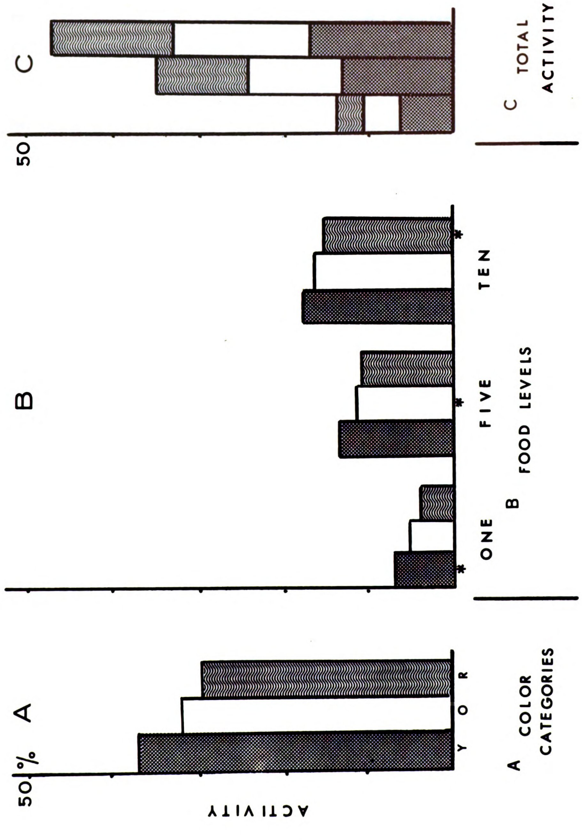
stations such that there were more snails present in them in the mornings than in the afternoons. But at each food level, there were no significant differences in densities among the morning observations; similarly among the afternoon observations, densities at each food level did not vary significantly.

Because the snail densities increased with the number of spinach particles available at the different food patches, it is unlikely that the original assignments of snails to the particular levels biased the counts. However, I checked each replicate for the distribution of snails from the three color categories; the variance: mean ratios of their densities (ca 0.3) at each food level were not significantly different from 1.0 ($P < 0.05$). Therefore the distribution of snails from each color category was random. If activity for a color category is taken as the percent of individuals tagged with that color that was present at the feeding stations, then clearly the colors did not affect their activity (Figure 3A), nor did the original assignment to a food level bias the activity of the snails (Figure 3B). Simply more snails occupied the higher food levels, without regard to their marking (Figure 3C).

Food Consumption

Although their average densities did not differ, the experimental populations ate (9 ± 3%) and damaged (34 ± 6%) significantly

Figure 3.--The relative proportions of snails from each color category (Y = yellow; O = orange; R = red) at: A--the feeding stations; B--each food level (* signifies the color category originally held at each food level); and C--total distribution of snails among food levels.


50%
A
Y
O
R
A COLOR CATEGORIES
ACTIVITY
B
ONE
FIVE
TEN
*
B FOOD LEVELS
C
50
C TOTAL ACTIVITY

less of their food resources than did the closed populations (24 ± 4; 51 ± 8% respectively; $P < 0.05$). But unrestricted to food patches, the snails in the experimental populations ate approximately 10% of the spinach particles at each food level, while the percent eaten by the restricted groups in the control populations decreased significantly with the number of food particles provided (43 ± 8; 30 ± 6; 13 ± 2% respectively; $P < 0.005$).

Food consumption, in terms of the number of particles eaten and damaged, neither increased nor decreased in the control populations over the experiment. This rather constant food consumption was in spite of the growth at the higher food levels, and the significant mortality among the snails at the low food level. However, among the unrestricted food levels, there was a linear increase in the number of food particles eaten at both the medium and the high food levels, and this despite the constant estimates of snail densities at each of these levels ($P = 0.005$).

Both damaged and intact spinach particles represented food to the snails, and after 24 hours of activity, the proportions of food still available was significantly higher in the experimental populations ($P < 0.005$; Figure 4). Most of these particles were intact (ca 56%), while in the controls, most of the available food particles were damaged (51%). But while this damage was consistent across food levels in the controls, it decreased significantly over food levels in the experimental populations ($P < 0.005$; Figure 4).

Feeding Activity

In the afternoons, 6 hrs. after being supplied with fresh spinach, approximately 40% of the snails in each population were feeding (Figure 5). But in the mornings, some 24 hrs. after fresh food was supplied and after 2 hrs. of light, the proportion feeding (56%) was significantly higher in the experimental populations ($P < 0.05$). In the control populations, about 40% of the snails were feeding, except at the low food level (17%) where usually little remained of the single spinach particle (Figure 4).

The unrestricted populations clearly differed in feeding pattern from the restricted populations, and this may be reflected in the relative impact each population had on its food resources. A consistent percent feeding in the restricted populations may have resulted in the relatively uniform damage to its food particles across food levels. In contrast, the diurnal fluctuations in feeding patterns for the unrestricted populations may have resulted in more efficient feeding in terms of the amount of time spent on the food particles and therefore in less food damaged and eaten.

Although significant in both populations, the correlations of feeding frequencies with snail densities, and with the amounts

Figure 4.--The percent of food particles remaining after 24 hrs. of feeding activity in the experimental (U) and control (R) populations. Stippled area is the percent damage; clear area is the percent intact.

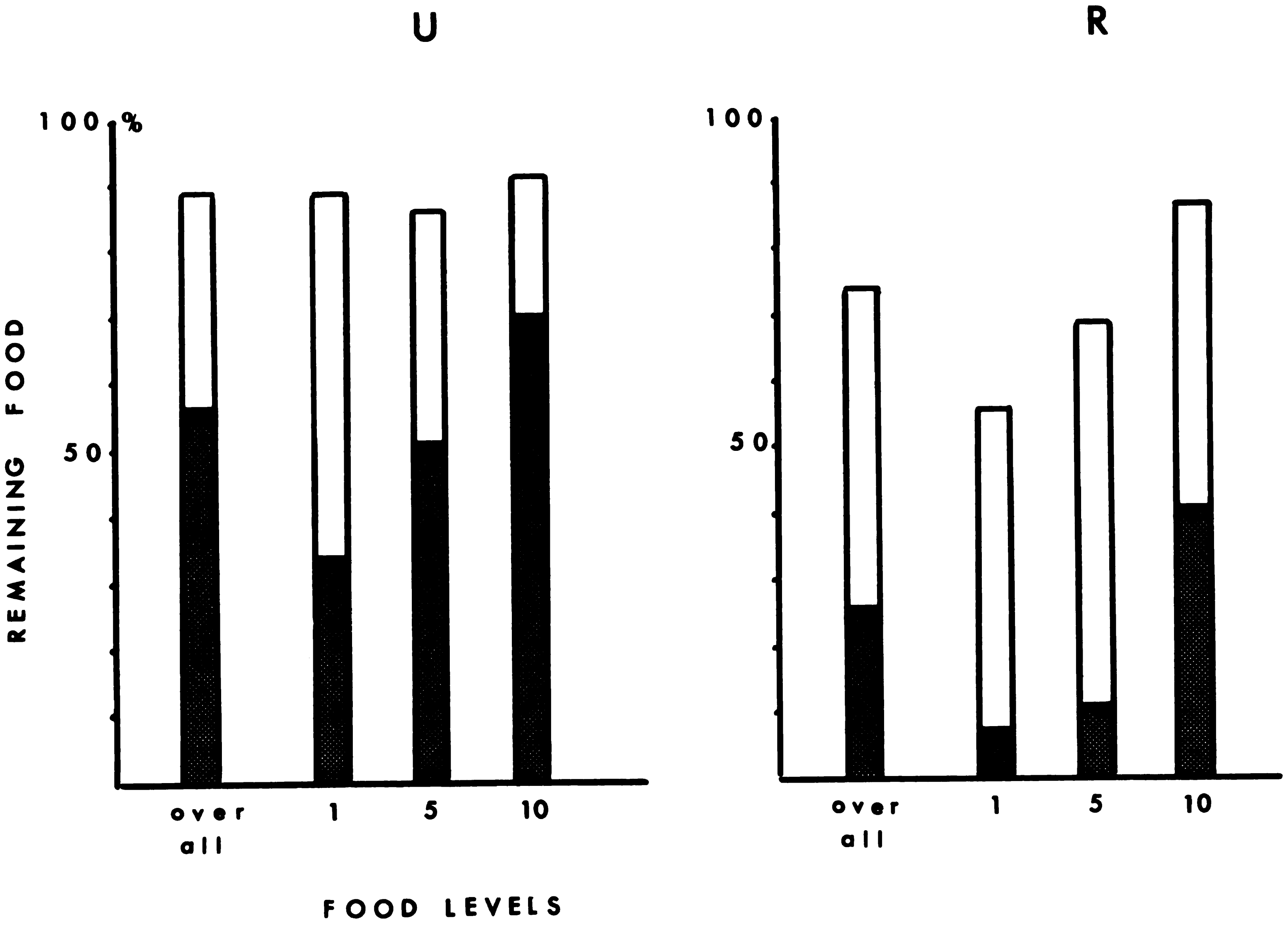
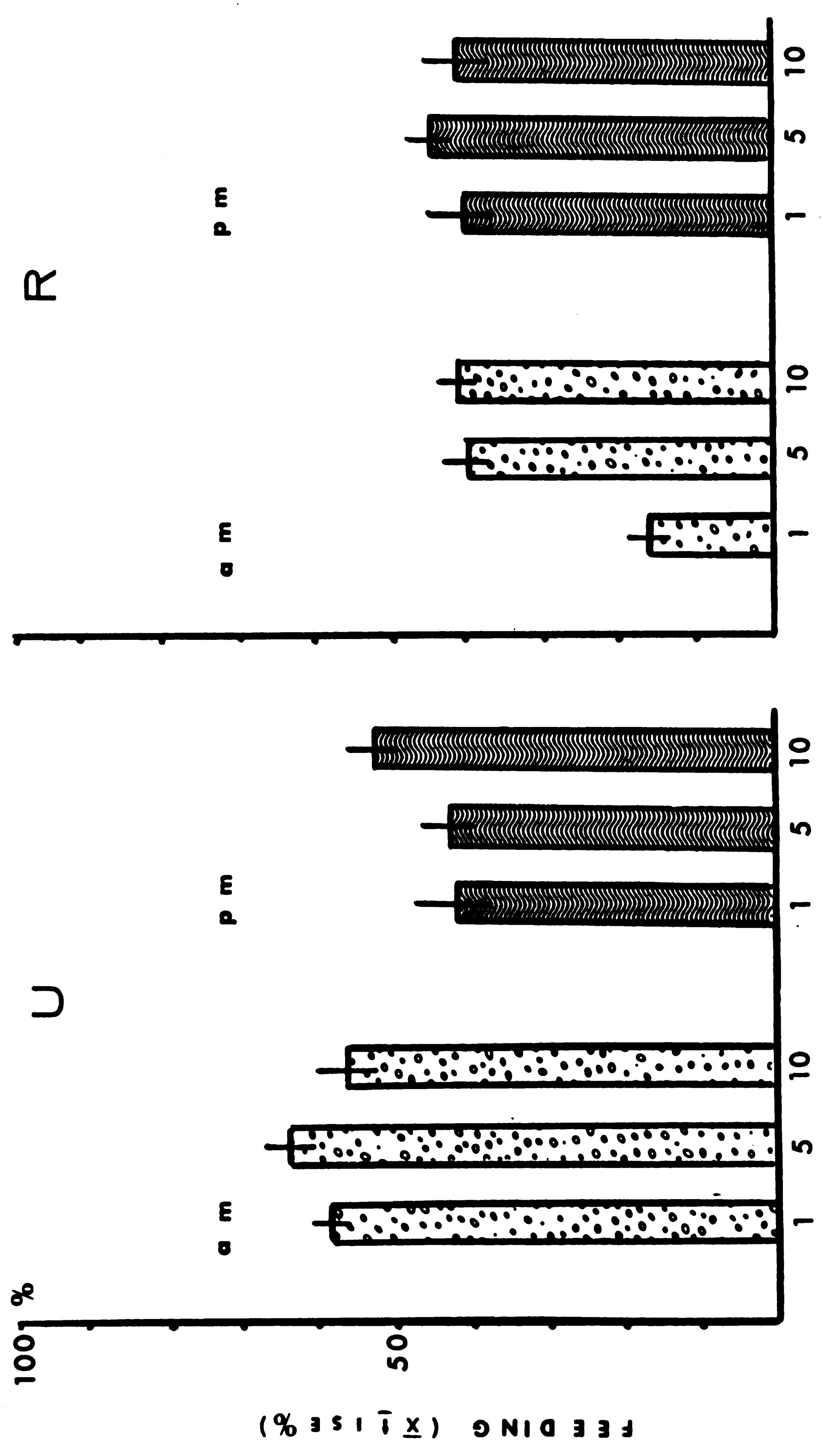

U
R
100 %
50
100
50
REMAINING FOOD
over all
1
5
10
over all
1
5
10
FOOD LEVELS

Figure 5.--Mean ± 1 S.E. percent feeding at each food level in the experimental (U) and control (R) populations in the morning (am) and afternoon (pm) observations.


FEEDING (X̄ ± SE %)
100
50
%
U
R
a m
p m
1
5
10

of food available are not only higher in the experimental populations, but they also both show greater homogeneity over food levels (Table 2). In particular, the correlations between feeding and available food particles reflect the fact that Physa conforms to the matching law (Baum 1974; Herrnstein 1970). This law predicts that the relative rates of engaging in alternative activities, such as feeding at different food levels, will be proportional to the relative rates of reinforcement, such as the number of spinach particles at these alternative food levels. Although this matching occurs in both populations, the correlation is closer in the experimental populations, whose snails closely matched their feeding activity to the available spinach particles at each food level (Appendix 2).

TABLE 2. Linear correlation coefficients between the number of snails feeding and: 1) the number of snails present; and 2) the condition of food particles after 24 hrs. of feeding activity. Bracketed coefficients are homogeneous (P = 0.05); ns = not significantly different from zero.

Number of Snails Feeding	Afternoon Observations	Morning Observations		
	Snail Densities	Snail Densities	Damaged Leaves	Intact Leaves
Experimental populations at				
low	0.6301	0.6350	0.3579	0.2329_{ns}
medium	0.6486	0.6677	0.4674	0.4513
high	0.8663	0.7463	0.3413	0.3254
Control populations at				
low	0.3252	0.1311	0.6181	0.1943_{ns}
medium	0.2988	0.1990	0.2436_{ns}	0.1373_{ns}
high	0.3090	0.0224_{ns}	0.4881	0.3607

DISCUSSION

Populational Responses

Knowing that dispersal is a basic factor in the regulation of animal numbers, I expected clear differences in populational responses between the unrestricted snails and those confined to fixed spatial and food resources in the controls. In particular, pond snails under restricted spatial and food resources should respond first in reproduction, then growth, and finally in adult mortality (Cooley 1973; Eisenberg 1966). For example, *Physa*'s reproduction is sensitive to culturing conditions: at fixed volumes and increasing snail densities, egg production is reduced, while doubling the culturing volume at fixed densities does not affect production but infertility increases (DeWitt 1954c). Yet here the presence or absence of dispersal in the large volume of the population trays altered neither the average egg production nor the degree of infertility. That is reproduction in the control populations was not affected by the relatively small volumes (130 ml) restricting groups of snails to fixed food levels, nor did egg infertility increase in the experimental populations with snails dispersing in the unrestricted tray volumes (18 liters).

That both populations produced about the same number of eggs might suggest that the snails were simply using energy reserves accumulated prior to the experiment. However, snails from the same culture, but in a separate, tandem experiment completely stopped producing eggs after three days of fasting, suggesting that no significant amounts of accumulated energy were available for reproduction in these snails.

In the size categories of snails used in the present experiment, Physa can grow at a rate of 2 mm/week (DeWitt 1954a); yet there was no significant growth, overall, in either population here. This lack of growth is probably due to the fact that the snails, raised under abundant and high quality food conditions in a large and uncrowded culture had already matured with the early and fast growth characteristic of pond snails under such rearing conditions (Eisenberg 1966, 1970).

Still, within the closed populations, two growth responses are evident. First, snails surviving at the low food level were smaller than the average size that was originally drawn for the experiment; this shows a higher survivorship but little growth for the smaller individuals restricted to limited food. Second, the snails at the medium and high food levels were larger than the other color categories in either population so that Physa responded to more abundant food by growing at the medium food level, and then with both growth and larger clutch sizes at the high food level.

Mortality among adults is the final characteristic affected by stress on pond snail populations and the stress of fixed food levels, particularly at the low food level, is apparent here. For although mortality did not differ on the average between the two populations, snails at the low food level in the controls had, toward the end of the experiment, clearly the highest mortality. But though smaller and fewer, this same group of snails produced an average number of eggs that was comparable to that of other snail groups in the restricted populations. However, dead snails remained in the feeding stations between observations and these were readily fed on by the other snails. Therefore, mortality at the low food level may have provided a high energy food and made possible the continued high egg production in spite of the limited amount of food and reduced snail densities there.

In sum, the effectiveness of dispersal in displacing the stress of food and spatial constraints on the population responses of an aquatic grazer are evident from these responses within rather than between the two populations. Without dispersal, and restricted to these limiting conditions, <u>Physa</u> first responds with lower survivorship in its larger individuals, but then at the medium food level, these restricted snails grow rather than increase their egg production.

Finally at the higher food level, this grazer produces larger clutches and grows rather than laying additional egg masses each day. Unrestricted, Physa disperses non-randomly among food patches, evidently displacing the stress of fixed food and spatial resources with uniform growth and survivorship among the unrestricted snails.

Behavioral Responses

For aquatic gastropods, some of the most interesting observations on dispersal come from work on their abilities to learn and the role of external stimuli, such as mucus trails, in their movements and orientations (Townsend 1973; Wells and Wells 1971). Snails produce mucus trails while moving and perhaps because they can follow these trails (Cook et al. 1969; Wells and Buckley 1972), some herbivorous snails orient to different kinds of food in the laboratory (Townsend 1973) and select among natural food substrates (Clampitt 1970; Pip and Stewart 1974). However, such selection has not been documented beyond the distribution of snails over different qualities of food, and has shown little of the variation in individual behaviors that regulates densities (Grime et al. 1970). Still, behavioral dichotomies, much as Wellington (1964) found in moth larvae, do appear in some snail populations where some individuals wander constantly while others return consistently to the same spots (Breen 1971; Lomnicki 1969; Pollard 1973).

Because the substrate over which a grazer moves is often its food, variations in both the quality and the quantity of foragable habitats is often indistinct, and the distribution of resource habitats unassessed in terms of grazing strategies. In the present experiment, the quality of food and its distribution were controlled by the use of a single food, spinach, at the feeding stations. Thus, how frequently these unrestricted snails encountered and used the spatial and food resources available to them describes their foraging in terms of the environmental grain of these population trays (Holling 1966; Pianka 1974). That is, this grazer used the spatial resources of the feeding stations as a course-grained resource, frequenting them with disproportionate densities. But the high correlation between feeding activity and the number of available food particles, clearly demonstrates that Physa exploited the food particles within these stations as a fine-grained resource.

If, by occupying the different feeding stations as course-grained resources, Physa shows some selectivity among these stations with different amounts of food, then its feeding behaviors could be interpreted broadly as a foraging strategy. Yet by regulating their densities at each food level on a diurnal cycle and over the experimental run, these unrestricted snails contradict the expectations of an optimal foraging strategy. That is, animals, such as an aquatic grazer whose major foraging component is searching rather than pursuing or capturing food, should generalize by consuming a broad diet, but then specialize somewhat in the most productive food patches (Pianka 1974). Diurnal fluctuations at the feeding stations contradict the expectation that having found a productive food patch, this grazer, like any consumer, would maximize its net resource gain by remaining at that patch.

Contrast this feeding behavior with the relatively consistent feeding in the control populations where about 40% of the snails were feeding at each daily observation. These restricted populations had imposed upon them an optimization of the profits and costs of searching; this optomization is reflected in the greater growth and larger clutch sizes at the higher food levels, and perhaps, by the continued high egg production even at the low food level.

Why then did the densities of snails fluctuate diurnally in the experimental populations? Perhaps it is because these unrestricted systems permitted the snails to disperse away from the feeding stations after they were disturbed during the morning cleanings. Or perhaps they showed a circadian rhythm involving feeding as other snails have (Malone and Nelson 1969); or variation in other activities, for example, over the day, oviposition occurs most frequently in the early morning hours for Physa (DeWitt 1954a). Of course, the snails may not have remained at the food patches simply because the food levels did not represent as sharp a gradient in size as I had intended. So that, though these snails foraged in a non-random manner, the accessibility of food and the levels used here may not have prompted an optimization in that foraging, as might be expected from models of particle size selection (Pianka 1974). Still, their non-random dispersal and the close matching of their feeding to available food shows that this grazer distinguishes among quantitative differences in an available food substrate.

CONCLUSIONS

Because the populational responses of pond snails are sensitive to extant food supplies (Eisenberg 1966), at the outset of this experiment two contrasting predictions were made. Neither prediction was met; rather, the two constraints: restriction to food levels, and unrestricted movements among food levels, resulted in similar, short-term responses for the two populations.

At the basis of the two contrasting predictions was the expectation that the experimental and control populations would exploit their food resources differently and according to their dispersal capabilities. This they did do, for although they both had the same potential carrying capacity in the food supplied to them, the experimental populations ate less of their food than did the controls. Effectively then, the experimental populations realized a higher carrying capacity as a result of their dispersal behaviors. Therefore, when able to disperse among different food levels, the grazer *P. gyrina* lost nothing in either reproduction or survivorship as a result of its movement, and in fact reduced its collective impact on its food resources.

APPENDICES

APPENDIX A

STATISTICAL MODEL

$$y_{ijkl} = \mu + A_i + B_{(i)j} + C_k + (AC)_{ik} + (BC)_{(i)jk}$$

$$+ D_i + (AD)_{il} + (CD)_{kl} + \left\{ BD_{(i)jk} + BCD_{(i)jkl} + E_{ijkl} \right\}$$

Source	Expected Mean Squares
A Treatments: A_i (experimental and control populations)	$\sigma^2 + \sigma_B^2 + (A_i^2)$
error a: replicates $B_{(i)j}$	$\sigma^2 + \sigma_B^2$
C Food levels: C_k	$\sigma^2 + \sigma_{BC}^2 + (C_k^2)/2$
Food levels in populations $(AC)_{ik}$	$\sigma^2 + \sigma_{BC}^2 + (AC)_{ik}^2/2$
error c: $(BC)_{(i)jk}$	$\sigma^2 + \sigma_{BC}^2$
D Time: D_l (13 days)	$\sigma^2 + \sigma_{BD}^2 + (D)_l^2/12$
Populations over days $(AD)_{il}$	$\sigma^2 + \sigma_{BD}^2 + (AD)_{il}^2/12$
Food levels over days $(CD)_{kl}$	$\sigma^2 + \sigma_{BD}^2 + (CD)_{kl}^2/24$
error d: $BD_{(i)jl}$	$\sigma^2 + \sigma_{BD}^2$
$BCD_{(i)jkl}$	$\sigma^2 + \sigma_{BCD}^2$

A_i : Populations: experimental and control; $i = 1,2$

$B_{(i)j}$: Replicates nested in populations: $j = 1,2,3,4,5$

C_k : Food levels: low (1 particle); medium (5 particles); high (10 particles); $k = 1,2,3$

D_l : Time: thirteen days of the experiment $l = 1,\ldots,13$

APPENDIX B

THE MATCHING LAW

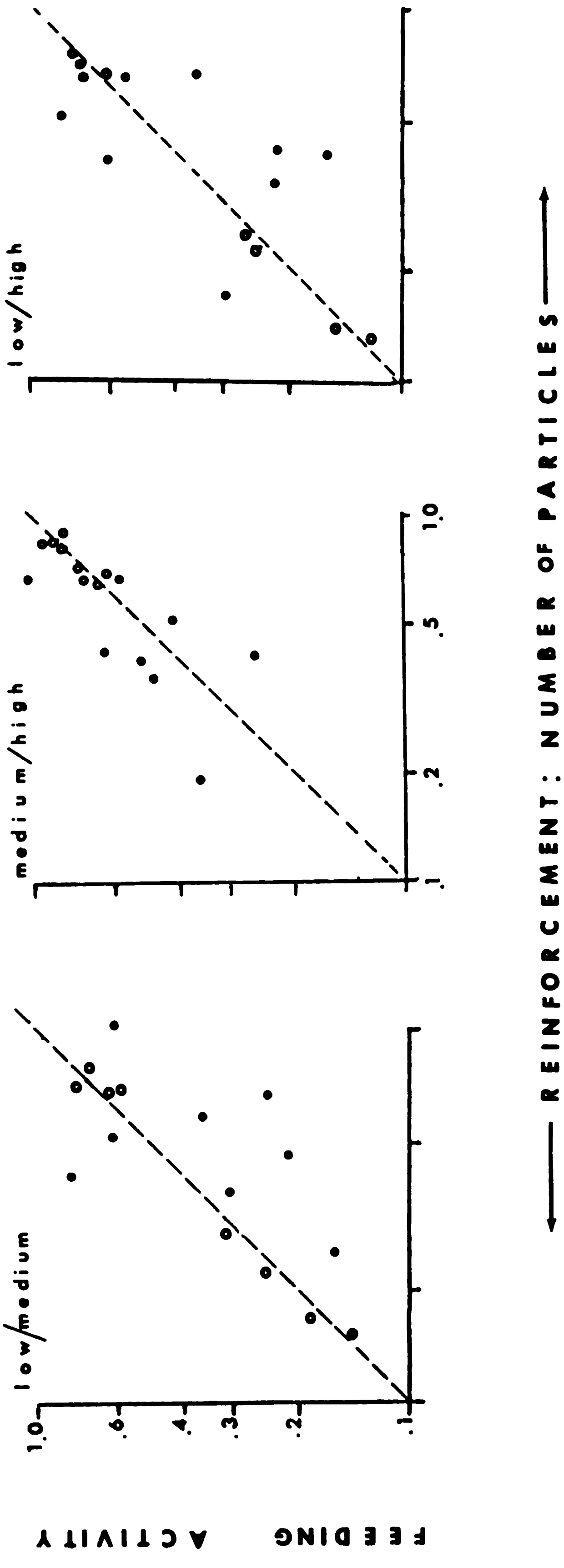
The matching law predicts that the relative rates with which an animal engages in two alternative activities will be proportional to the relative rates of reinforcement from such activities (Baum 1974; Herrnstein 1970). For example, given two patches of food with different amounts of food in them, an animal should feed at them in proportion to the amount of food it can receive in each. In terms of the present experiment, if the number of snails feeding at the ith food level is (f_i) of the total number of snails present in the population (n), then the relative feeding activity at the ith food level is $F_i = \frac{f_i}{n}$. Similarly if the number of spinach particles present as intact and damaged at the ith food level is (a_i) of the total number of particles fed to the population (r = 16), then the relative reinforcement ratio at the ith food level is $R_i = \frac{a_i}{r}$. Under the matching law, the relative amount of feeding activity (F_i) and the reinforcement rate (R_i) at the ith food level will be proportional to those rates at the jth food level:

$$\frac{F_i}{R_i} = \frac{F_j}{R_j} \;(1) \qquad \text{or} \qquad \frac{F_i}{F_j} = \frac{R_i}{R_j} \;(2).$$

The proportionality proposed by the matching law in equation (2) is tested graphically with a log-log plot of the ratios: the feeding activity at two alternative food levels is plotted on the ordinate, the reinforcement plotted on the abscissa. If there is a perfect matching or proportionality between the activity and reinforcement ratios, then for every change in the relative reinforcements at two food levels, there will be a proportional change in the relative feeding activity at these two food levels. In other words, the plotted data will lie on a 45° line through the origin of the graph (Baum 1974). For the matching function to be non-trivial, the feeding frequency (activity) must exceed the number of food particles (reinforcement) Hernnstein 1970). This caveat is satisfied here as the snails constantly scrape the substrate over which they move, so that feeding activity (scraping) far exceeds the reinforcements (spinach particles on which to feed) at each food patch. Therefore, in this experiment there are alternative feeding opportunities, not only between the tray areas where no spinach particles are present and the feeding stations with spinach, but also among the feeding stations themselves where different numbers of spinach particles are available.

In Figure B1, the relative feeding activities (F_i/F_j) and food reinforcements (R_i/R_j) are plotted for the experimental (opened circles) and control (dark circles) populations. These comparisons are plotted for the first eight days of the experiment, after which most of the points were redundant and therefore not plotted as they

Figure B 1.--The matching between a) the proportion of snails feeding at two food levels (ordinate) with b) the proportion of food particles present at these same food levels. Opened circles = experimental populations; closed circles = control populations.


low/medium
medium/high
low/high
1.0
.6
.4
.3
.2
.1
.1
.2
.5
1.0
REINFORCEMENT : NUMBER OF PARTICLES
FEEDING ACTIVITY

simply cluttered the plots (especially the comparisons between the medium and high food levels).

Two points are obvious from Figure B1. First, snails in the experimental populations closely matched their feeding activities to the spinach particles available to them. On the other hand, snails restricted to fixed food levels in the control populations showed much less correlation between their feeding and the number of food particles. These low correlations occur in both directions: a few snails feeding in the presence of many spinach particles; and a large number of snails feeding on few spinach particles. Second, the close matching of feeding activity to reinforcement levels in the experimental populations is consistent across all three food levels, but in the control populations, the closest matchings appear at the medium/high food comparisons. However, even in these comparisons, the matching is not close in the control populations.

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