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ON THE COMPLEXITY OF A SIMPLE ENVIRONMENT: COMPETITION, RESOURCE PARTITIONING AND FACILITATION IN A TWO-SPECIES *DROSOPHILA* SYSTEM

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[Plates 1 and 2]

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An experimental system for studying ecological interactions between *Drosophila* species is described and the results of an extensive series of long-term experiments involving *D. hydei* and *D. melanogaster* are presented. These reveal a variety of types of interaction and a variety of mechanisms producing stable coexistence. Some of the experimental results serve to confirm the predictions of competition theory: in one environmental régime *D. hydei* and *D. melanogaster* coexist, despite interspecific competition, because of resource partitioning in the form of a difference in larval depth distributions. Other results urge the development of new bodies of theory: in a different environmental régime, *D. hydei* and *D. melanogaster* exhibit a previously unrecognized (+, −) kind of interaction for which I propose the name *contramensalism*. This kind of interaction is of interest because it can have a balancing effect and can produce stable coexistence of closely related species in a way that is quite distinct from classical resource partitioning.

1. Introduction

One of the central issues in the theory of interspecific competition is what *mechanisms* are capable of causing stable coexistence of competing species. Mechanisms that have been suggested include resource partitioning (see Schoener (1974) for a review), spatial aggregation (Shorrocks *et al.* 1979), non-transitive competitive abilities (Gilpin 1975), genetic feedback (Pimentel *et al.* 1965) and seasonal presentation of resources (Stewart & Levin 1973; Koch 1974). The conventional view on the efficacy of these various mechanisms can be stated as 'resource partitioning is the predominant stabilizing mechanism in nature', and this statement is in fact one version of the competitive exclusion principle. Other versions are more dogmatic, such as Hardin's (1960) statement that resource partitioning (or ecological differentiation as he calls it) is the 'necessary' cause of coexistence rather than just the predominant one.

It must be stressed that the question of mechanism logically precedes the question of what precise quantitative conditions are required if coexistence is to ensue. For example, if species coexist through resource partitioning, then it may (or may not) be possible to formulate general conditions for coexistence in terms of limiting similarity (see May & MacArthur 1972; Abrams 1983). However, such formulations are totally inapplicable to coexistences caused by (for example) non-transitive competitive abilities.

Studies of competing populations in the laboratory have a clear role to play in the debate about mechanisms of coexistence. It is in laboratory systems that it is easiest to demonstrate that a particular stabilizing mechanism can actually work in practice. Surprisingly, previous laboratory studies on competition have largely failed in this respect, because they have been unable to give a clear identification of which of the various proposed stabilizing mechanisms is responsible for an observed state of coexistence. Workers supporting the conventional mechanism, i.e. resource partitioning, have tended to assume this mechanism rather than to actually demonstrate it, the most notable omission from such studies often being a lack of data quantifying the proposed form of partitioning (see, for example, Gause 1935; Crombie 1945). Workers claiming that an observed state of coexistence was *not* caused by resource partitioning have not provided a clear demonstration of which alternative mechanism is acting (Ayala 1969, 1970, 1971; Levin 1972). We are a long way from being able to determine the truth or otherwise of the competitive exclusion principle which attempts to *generalize* about stabilizing mechanisms if we cannot conclusively identify the mechanism acting in any particular case, and clearly the distinguishing of one mechanism from another is even more difficult in the field than in the laboratory.

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The aim of this paper, together with a related one (Arthur & Middlecote 1984*b*) is to demonstrate the stabilizing mechanisms acting to maintain observed coexistences of *Drosophila hydei* and *D. melanogaster* in laboratory cultures. As will be seen, the situation turned out to be highly complex despite the use of a simple 'two species, one resource' system, in that slightly different environments were characterized by fundamentally different stabilizing mechanisms.

One mechanism excluded from the list given above but that turned out to be important in one of the experiments reported here is facilitation. In this process, one or both species alter(s) the environment in a way that favours the alternative species. The reason for the omission of facilitation from the list of mechanisms acting to stabilize systems of competing species is that if competition is defined as a $(-, -)$ interaction (see Odum (1953) and Williamson (1972)), then facilitation and competition are mutually exclusive. Thus although facilitation can cause a state of stable coexistence of ecologically interacting species, its presence indicates that the interaction is not a competitive one, at least under the $(-, -)$ definition.

In fact the experiments reported here differed not only in the stabilizing mechanism but also in the nature of the interaction itself. Some mixed cultures of *D. hydei* and *D. melanogaster* showed no interaction (0, 0), some showed conventional competition $(-, -)$, and others showed a novel, non-trophic $(+, -)$ interaction, which I have termed *contramensalism*. This variation both in the nature of the interaction and in the type of stabilizing mechanism operating to produce coexistence shows how complex a 'simple laboratory system' can turn out to be when analysed in detail. This fact urges a cautious approach to drawing conclusions from studies of natural systems, involving, as they do, more resources, more species utilizing them, and more variation in environmental factors such as temperature and humidity that can greatly affect the outcome of competitive, and other, interactions.

2. The *Drosophila* experimental system

2.1. *Materials and methods*

In long-term competition experiments there are different ways of renewing the resource. In work with insect populations the two main forms of renewal are serial transfer (see Ayala 1969) and continuous culture (as used in the experiments reported herein). Serial transfer is a useful technique if populations are kept in bottles, and Ayala's method was to keep several bottles of different ages, periodically transferring newly emerged adults into the newest bottle. A problem with this method, however, is that competition between different life-stages (e.g. between different larval instars) is reduced, relative to competition within any one of them. This may affect the likelihood of obtaining stable coexistence; specifically, it may artificially increase the probability of such an outcome, since inter-instar competitive effects are likely to be highly asymmetric and destabilizing. The problem is avoided with the continuous culture method, where a single population cage contains all of the life-stages.

The population cages used in the experiments presented here (and also in the experiments of Arthur (1980*a*, *b*), and Arthur & Middlecote (1984*a*, *b*)) consisted of clear plastic boxes (17 cm × 11 cm × 6 cm) with six glass bottles screwed into their undersides (see figures 1 and 2, plate 1). These cages are large enough to allow substantial populations to build up (around 200–2000 adults, depending on the amount of resource, and many thousands of larvae), but small enough to allow the several replicate cages of each experiment to be maintained in a small amount of incubator space. Incubators were kept at 25 ± 1 °C with a light-régime of 16 h light,

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8 h dark throughout the experimental programme (except for one experiment, described later, which was run entirely in the dark). The relative humidity was not controlled but fluctuated quite narrowly in the 25–30% RH band.

Maintenance of population cages over long periods of time (up to a year) was very simple, and involved only three procedures: resource renewal, cage changing, and, in experimental but not stock cages, population counts. With regard to resource renewal, the oldest two bottles were replaced weekly with fresh ones containing only instant *Drosophila* medium (IDM; obtained from Griffin & George, Gerrard Biological Centre, Sussex) hydrated with distilled water. Each bottle thus remained in the cage for three weeks, except at the beginning of the experiment where slight departures from the 'equilibrial' pattern of bottle-changing were necessary. Cages were changed approximately every 8 weeks because of fouling produced by the flies' activities. Population counts were made every 2 weeks by anaesthetizing with CO_2, and temporarily removing from the cage, the whole adult population. Because only adults were counted, the count was a partial one in the sense of Varley *et al.* (1973), but all counts were of the whole adult population rather than a sample of it. The counts, made with a simple hand-counter, were accurate to about ± 5 flies in a population of 500, which is a negligible error compared to those produced by sampling.

While the population-cage system used is clearly a very artificial environment, it does simulate rather well certain attributes of natural habitats. In particular, much has been made of the importance, in competition, of 'discrete, ephemeral resources' (see Shorrocks *et al.* 1979; Atkinson & Shorrocks 1981), especially in relation to species that utilize rotting fruits–as many *Drosophila* do. The characteristic of such resources is that they appear suddenly in discrete patches, deteriorate fairly quickly and eventually disappear again. These are precisely the characteristics of the resource bottles in the *Drosophila* population cages used here.

2.2. *Stocks*

Two species were used in the experiments to be described–*Drosophila hydei* and *D. melanogaster*. Neither had been deliberately inbred before my receiving them, and after receipt both were kept in stock cages allowing large population numbers to be maintained. Thus both stocks were genetically variable, and indeed the *D. hydei* stock evolved, with respect to pupation site, in an experiment described in Arthur & Middlecote (1984*a*). However, no evolutionary changes were observed in the experiments reported herein, and these experiments are thus informative on population-dynamic aspects of competition rather than on evolutionary ones.

While the *D. hydei* stock used was wild-type, the *D. melanogaster* stock was marked with the recessive white-eye mutation *w* (X chromosome, position 1.5: see Lindsley & Grell 1968). This genetic marker was initially used to facilitate distinguishing *D. melanogaster* from its sibling species *D. simulans*, which was used in some other competition experiments not described here. The effect of the *w* gene is to reduce fitness generally, and the *D. melanogaster w* stock used here is less well able to compete with *D. hydei* than is the wild-type *D. melanogaster* strain used in the experiments of Arthur & Middlecote (1984*b*). However, because the *D. melanogaster w* stock was used in all the competition experiments reported in the present paper and in all the associated single-species controls, effects that emerge from comparison of different experiments or of an experiment with a control cannot be a consequence of the marker.

It should be stressed that *D. hydei* and *D. melanogaster* are in different species groups, and

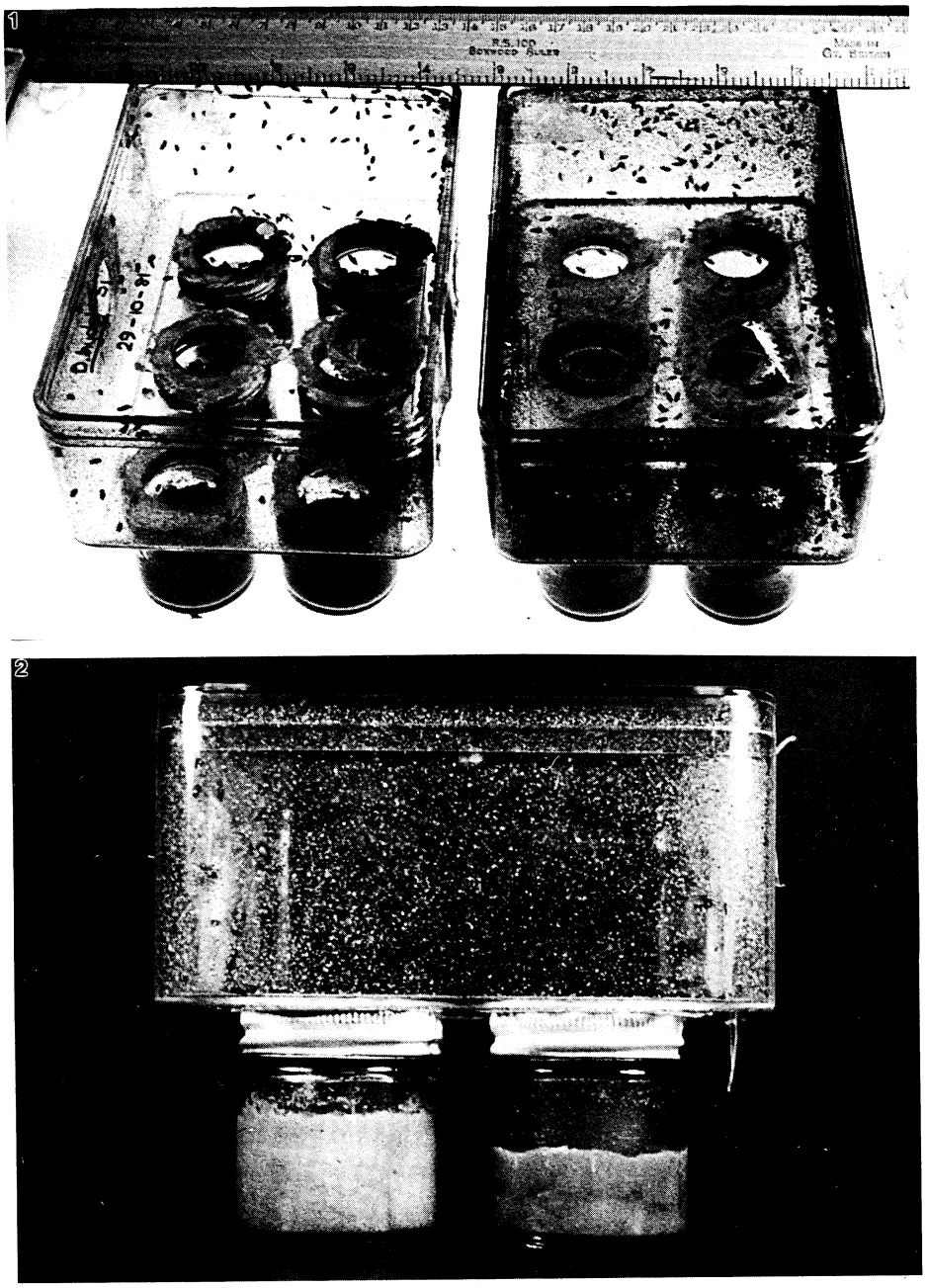

FIGURE 1. Population cages. View from above with adults visible.

FIGURE 2. End view of population cage. Large larvae and pupae are just visible in the right-hand resource bottle.

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indeed in different subgenera, within the genus *Drosophila* (Patterson & Stone 1952). Not only are they different morphologically (*D. hydei* being much larger), but they also differ at the level of the gross karyotype, *D. hydei* having $2n = 12$ in contrast to *D. melanogaster*'s $2n = 8$. There is little possibility of hybridization between two such species, and the lack of interbreeding was confirmed by a no-choice mating experiment. Thus the only interaction that takes place in mixed cultures is an ecological one.

The taxonomic, morphological and karyotypic differences between *D. melanogaster* and *D. hydei* are accompanied by ecological differences which are relevant to the experiments described herein. One notable difference is in the generation time. At 25 °C the generation time of *D. melanogaster* is 10–14 days, that of *D. hydei* about 14–24 days. All developmental phases of the *D. hydei* lifecycle – egg, larva and pupa – contribute to the lengthened generation time. Also, when adult, male *D. hydei* take up to 9 days to become fertile (Hess 1976), in contrast to *D. melanogaster* males, which are fertile very shortly after emergence.

2.3. *Experimental design*

The main series of experiments were two-species, multi-generation 'competition' experiments and their single-species controls. These will be collectively referred to as the 'long-term experiments'; they lasted for either 30 or 50 weeks – or approximately half that number of generations, since at 25 °C a generation lasts about a fortnight (*D. hydei* slightly more, *D. melanogaster* slightly less). In addition to the long-term experiments, several different short-term experiments were conducted, mostly in glass vials, for a variety of reasons. These will be described individually as they arise in §§4 and 5. The standard procedure for long-term experiments is described below.

(i) *Two-species long-term experiments*

All cages were set up with $10♂ + 10♀$ of one species and $40♂ + 40♀$ of the other. Thus each cage had an overall starting density of 100 flies per cage, an initial species-frequency (expressed as percentage *D. melanogaster*) of 20% or 80%, and a 1:1 sex ratio within each species. Each experiment consisted of six cages: $3 \times 20\%$ and $3 \times 80\%$. Divergent starting frequencies were employed to facilitate the search for equilibria.

(ii) *Single-species controls*

These cultures were established in triplicate, the three cages of each experiment each being started with 50 flies: $25♂ + 25♀$. This initial density was chosen as it is midway between the starting densities of 20 and 80 flies per cage used in the two 'halves' of each two-species experiment. The single-species cultures were used for the estimation of K values and, from these, of competition coefficients (see §3).

(iii) *The overall experimental programme*

The overall programme consisted of four long-term 'competition' experiments and eight single-species controls. An outline of the programme is given in table 1. The first experiment was started in June 1980 and the final one terminated in October 1984, with many experiments being run in parallel throughout the intervening 4 to 5 year period. The results of this series of experiments, together with associated short-term vial experiments, are given in §§3, 4 and 5.

Table 1. Outline of experimental programme

experiment code*	species	mass of IDM per bottle / g	duration / weeks	no. of cages	light régime (h light:h dark)
HM5	*mel* + *hyd*	5.0	50	6	16:8
HM2L	*mel* + *hyd*	2.5	50	6	16:8
HM2D	*mel* + *hyd*	2.5	30	6	0:24
HM1	*mel* + *hyd*	1.5	50	6	16:8
H5	*hyd*	5.0	30	3	16:8
H2	*hyd*	2.5	30	3	16:8
H1A	*hyd*	1.5	30	3	16:8
H1B	*hyd*	1.5	30	3	16:8
H1C	*hyd*	1.5	30	3	16:8
M5	*mel*	5.0	30	3	16:8
M2	*mel*	2.5	30	3	16:8
M1	*mel*	1.5	30	3	16:8

* M, *melanogaster* monoculture; H, *hydei* monoculture; HM, mixed culture. L, light (i.e. 16:8); D, dark (0:24). A, B, C refer to different amounts of water added to the IDM: this variable is discussed in §5.

3. Demonstration of interspecific competition

3.1. *Introduction*

It is conventional, in long-term experiments on competition, to optimize physical conditions such as temperature, to exclude as far as possible all predators and parasites, and to insert a finite amount of food at regular intervals. In such a system it seems likely that populations will be resource-limited rather than either being regulated by a density-dependent parasite or fluctuating irregularly (due to adverse physical conditions) below *any* equilibrium. Since it is also usual to include only a single type of resource, two species in a population cage are likely to be limited by the same resource and so to be in competition. Indeed, many workers have assumed this rather than testing experimentally that competition is actually occurring. However, competition, defined as a $(-, -)$ interaction (Odum 1953; Williamson 1972), is not a necessary consequence of the type of population culture described above. Also, the commonness of competition relative to other types of interaction, such as amensalism, is being increasingly questioned (Lawton & Hassell 1981, 1984). It is thus of interest to measure the strength and direction of the interaction coefficients and hence to establish whether competition, or some other kind of interaction, is taking place.

One way to do this is to measure the coefficients α and β from the Lotka–Volterra model:

$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = r_1 N_1 \left(\frac{K_1 - N_1 - \alpha N_2}{K_1}\right),$$

$$\frac{\mathrm{d}N_2}{\mathrm{d}t} = r_2 N_2 \left(\frac{K_2 - N_2 - \beta N_1}{K_2}\right).$$

Here, α measures the effect per individual of species 2 on population growth or equilibrium population size in species 1, while β is the effect per individual of species 1 on species 2's population. In the experiments to be described shortly, α measures the effect of *D. hydei* on *D. melanogaster* and β the converse; thus *D. melanogaster* is the experimental equivalent of the model's 'species 1'.

If a state of stable coexistence is reached, α and β can be estimated from the single-species carrying capacities (K) and the mixed-species equilibrium population sizes ($\hat{N}$) as $\alpha = (K_1 - \hat{N}_1)/\hat{N}_2$ and $\beta = (K_2 - \hat{N}_2)/\hat{N}_1$. A derivation of this result is given by Ayala (1969). Of course, all individuals are not identical in their effect on the alternative species, as the rather unrealistic Lotka–Volterra model assumes. But if we interpret α and β as *averages* rather than constants this difficulty is avoided. Alternatively, we can simply define the competition coefficients as these averages without reference to the Lotka–Volterra model.

3.2. *Estimation of K and $\hat{N}$*

In theory the estimation of these parameters should be very straightforward. In practice a difficulty arises because it is not immediately apparent when the growth phase ceases and the equilibrium phase begins. The problem is that population growth in *Drosophila* cultures is often an erratic process, with some early generations showing declines even though population sizes are well below their equilibrium, and some later ones showing considerable growth when populations appear to be already above their equilibrium

There are two possible solutions to this problem. One is to inspect each graph of population size separately and to decide when each population has 'peaked'. The other is to employ a general rule for all experiments. The latter solution was adopted because the problems associated with an experimenter's omitting a chosen subset of the data are less severe than if the alternative solution is adopted. Equilibrium conditions were considered to start at week 10 (generation 5); inspection of figures 3 and 4 shows that this is a reasonable choice. K and $\hat{N}$ were obtained by averaging data from the period week 10 to week 30 inclusive, the later limit being necessary because, although most two-species experiments extended to week 50, the single-species cultures all terminated at week 30. It makes sense to compare K and $\hat{N}$ calculated for similar periods because of the possibility that evolutionary adjustment of a stock to its population cage permits a gradual rise in $\hat{N}$ in the long term, after 'ecological' population growth has ceased.

In §3.3 below, all graphs of population size against time show lg N, for the reasons given by Williamson (1972, ch. 1) – most importantly that equal multiplicative population changes appear equal on the graphs. The calculations of K, $\hat{N}$, α and β, however, are based on the original (i.e. non-logged) data, as is appropriate. Tables of the original data on population sizes are omitted from the text, but may be found in the Appendix. (One additional aspect of the data that emerges from the Appendix is a tendency for *D. hydei* population sizes to be larger in the cages at the front of the incubator (the C cages). This may be due to a micro-gradient of temperature.)

3.3. *Results*: α *and* β

Of the four mixed-culture experiments HM5, HM2L, HM2D and HM1 (see table 1), three were used to calculate α and β. The fourth, HM2D, was not used for this purpose because no single-species cultures were run in total darkness and there are thus no K values corresponding to the $\hat{N}$ values of that experiment. The three other experiments form a series of gradually decreasing amount of resource per bottle (5 g, 2.5 g, 1.5 g), which might be expected to correspond to a gradually increasing intensity of competition. As will be seen shortly, this expectation was not realized and the actual situation could hardly have been predicted.

(i) *The 5 g resource cultures*

The results of both mixed and single-species cultures with 5 g of resource per bottle are shown in figure 3, each trajectory representing the mean value of three replicate cages. (Data for individual cages are given in the Appendix.) As can be seen, the mixed-species $\hat{N}$ values oscillated above and below the K values over the week-10 to week-30 period, indicating lack of any interaction in the mixed-species cultures. This is confirmed by calculation of 'competition' coefficients:

$$\alpha = +0.01, \quad \beta = -0.23.$$

The K and $\hat{N}$ values used to calculate α and β here, as well as in the 2.5 g experiments, are given in table 2.

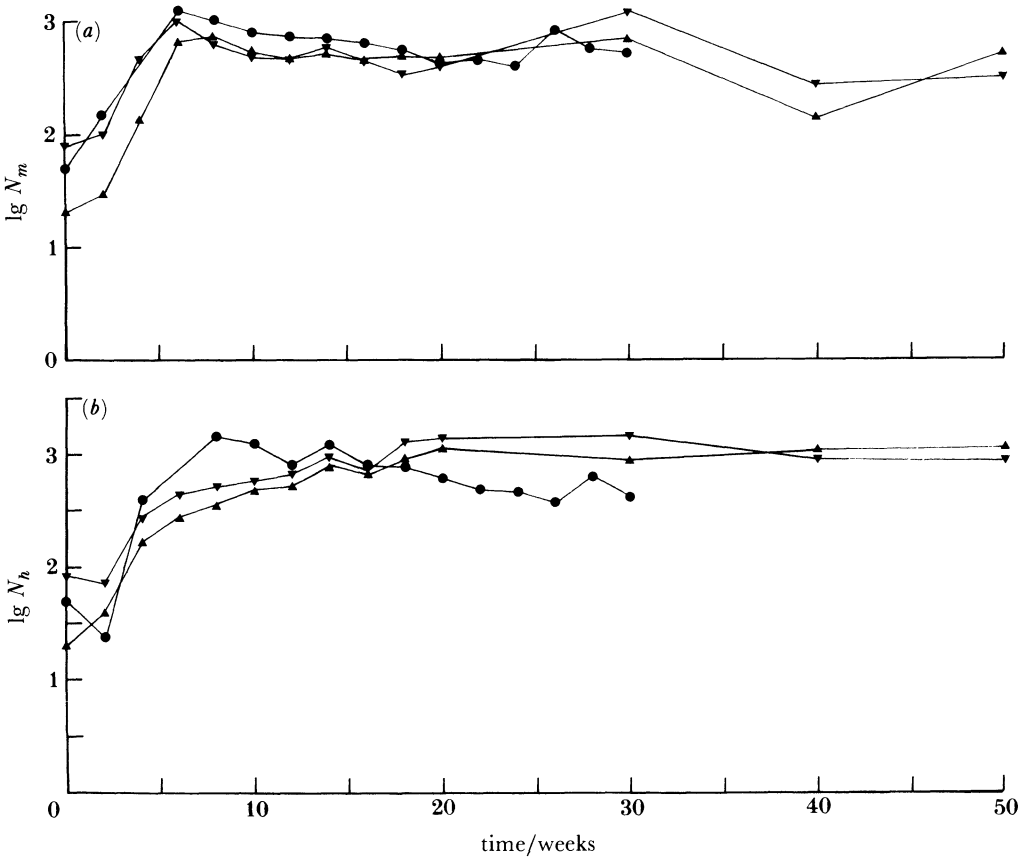

FIGURE 3. Population sizes in the 5 g resource system: (*a*) *D. melanogaster*; (*b*) *D. hydei*. In this and all subsequent figures logarithms are to the base 10. ●, Monoculture; ▲, mixed culture (cages started with 20% of the species concerned); ▼, mixed culture (cages started with 80% of the species concerned).

As can be seen, the coefficients are small in absolute value. The calculated coefficients for this and later experiments all have absolute values either in the 0–0.25 band or in the over 0.50 band, and it is tempting to assume that the former are due to sampling variation and the latter represent real effects. However, the result of −0.23 is perhaps too large to write off as a chance effect without some formal test of its significance. A problem arises here because there is no *direct* way to test the significance of the departure of a single coefficient from zero. What

TABLE 2. K AND $\hat{N}$ VALUES USED IN CALCULATION OF COMPETITION COEFFICIENTS FOR THE 5 g AND 2.5 g SYSTEMS

resource quantity	equilibrium population numbers*			
	D. melanogaster		*D. hydei*	
g	K	$\hat{N}$	K	$\hat{N}$
5.0	547	536	724	849
2.5	593	151	459	358

* K, carrying capacity in monoculture; $\hat{N}$, equilibrium numbers in mixed culture.

can be done, as an indirect test, is to see whether the appropriate single-species K values and mixed-species $\hat{N}$ values are significantly different.

A test of this kind can be performed by using the statistical package GLIM (General Linear Interactive Modelling – see Baker & Nelder 1978). A model of the data is built that first takes out effects due to time and then those due to 'culture' (i.e. mono against mixed). The drop in deviance occurring when culture effects are allowed for is distributed as a χ^2, as is the residual deviance not explained by the most complete GLIM model. To test for significance of the culture effect, the ratio of drop in deviance per degree of freedom due to 'culture' to residual deviance per degree of freedom is calculated. This is distributed as an F ratio, and so the probability of obtaining any particular value can be easily determined. The F ratios for the 5 g experiment were not significant (even at the 10% level), and the 'interaction' is apparently a (0, 0) one – in other words, there is *no* interaction. This rather unexpected result leaves open the question of how population sizes were limited in the 5 g cultures. Further experiments would be required to elucidate the mechanism of limitation.

(ii) *The* 2.5 g *resource cultures*

In this case the competition coefficients, calculated from $\hat{N}$ and K values given in table 2, are as follows:

$$\alpha = 1.23, \quad \beta = 0.67.$$

These high positive values reflect substantial *reduction* of equilibrium population sizes in mixed culture. (Recall that competition models have a component $-\alpha N$, so that negative values of α turn into positive $-\alpha N$ values and hence reflect a '+' effect of one species on the other.) The interaction is asymmetric in that the inhibitory effect of *D. hydei* on *D. melanogaster* is about twice as great as the opposite effect, but it is clearly a competitive interaction rather than an amensal one. It should be noted that the large effect of *D. melanogaster* on *D. hydei* (0.67) is almost invisible in the corresponding graph (figure 4). This is because whereas 0.67 is a large effect *per individual*, the equilibrium number of *D. melanogaster* in mixed culture is small, and hence its *population* has a relatively small overall effect on the *D. hydei* population. This point illustrates a difficulty in the indirect testing of the significance of interaction coefficients, as described in the previous section.

(iii) *The* 1.5 g *resource cultures*

The nature of this interaction (i.e. whether it takes a (−, −) form or some other) and the stabilizing mechanism permitting coexistence under it are rather difficult to separate, and will

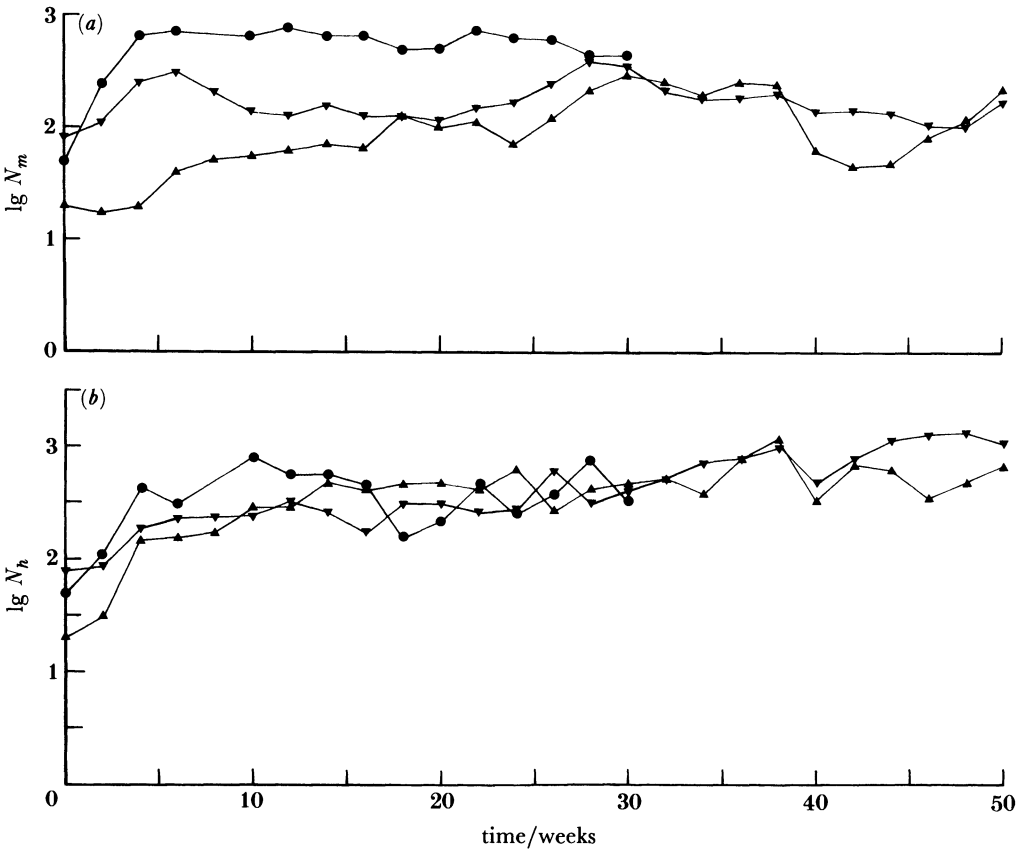

FIGURE 4. Population sizes in the 2.5 g resource system: (*a*) *D. melanogaster*; (*b*) *D. hydei*. ●, Monoculture; ▲, mixed culture (cages started with 20% of the species concerned); ▼, mixed culture (cages started with 80% of species concerned).

be dealt with together in §5. Suffice it here to say that the anticipated strong (−, −) interaction did not materialize; rather, an unexpected and novel type of (+, −) interaction was discovered.

4. Stable coexistence with resource partitioning

4.1. *Graphical presentation of data*

Population sizes of the two species in the 5 g and 2.5 g systems have already been given, in logarithm form, in figures 3 and 4. In this section, where demonstration of competitive equilibrium rather than of competition itself is the aim, different forms of presentation are appropriate. Admittedly, the fairly constant lg N values from week 10 onwards (figures 3 and 4) are suggestive that equilibrium has been reached in all the mixed-species cultures. However, a stronger case for stability can be made by re-plotting the data either in terms of species-frequencies or as phase plane diagrams with axes N_1 and N_2.

In the past, different groups of workers have favoured different presentations. Population biologists whose interests extend through population ecology and population genetics have mostly opted for species-frequency diagrams, perhaps because of the analogy of species frequency and gene frequency (see, for example, Ayala 1971; Levin 1972; Arthur &

Middlecote 1984*a*,*b*). Ecologists, on the other hand, have mainly used phase-plane diagrams (see, for example, Gause 1935; Crombie 1945). Both forms of presentation have their advantages and their drawbacks. The condensation of numbers into frequencies makes equilibria particularly easy to detect in some cases. However, if systems with the same frequency but different overall densities behave differently, the use of frequencies is clearly undesirable and represents an *over*-condensation of the data.

Perusal of the literature on competition suggests that each 'school' refers disproportionately often to papers in which its preferred form of presentation is employed. In attempt to avoid only being referred to by one group of workers, and because both forms of presentation have their strengths, I have plotted the data in both ways.

4.2. *The* 5 g *resource experiment*

The results of this experiment are shown graphically in figure 5 (species frequencies) and figure 6 (an N_1/N_2 phase plane). These results are presented mainly to illustrate that the growth and stabilization of two non-competing sympatric populations can look very similar, when plotted in these ways, to the growth and stabilization of competitive ones (see §4.3). That is, species-frequency and phase-plane diagrams both make a pair of separate stable points (K_1 and K_2) look like a stable competitive equilibrium despite the fact that the population dynamics are essentially behaving independently. The results of the 5 g experiment tell us nothing about interspecific competition, but they do make it very clear that the results given in this section and the next need to be interpreted jointly with the demonstrations of the nature of the interactions, given in §3.

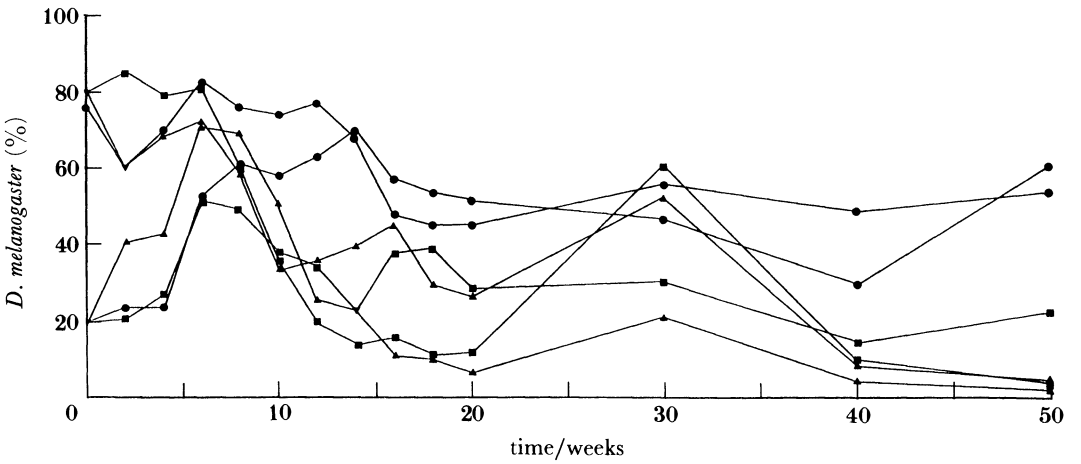

FIGURE 5. Results of experiment HM5, plotted as species-frequency against time.

4.3. *The* 2.5 g *resource experiments*

Figures 7 and 8 show the results of the first 2.5 g competition experiment (HM2L). These appear similar to the results of the 5 g experiment, but the interpretation is now different as we are dealing with a $(-, -)$, as opposed to a $(0, 0)$ interaction. Three points can immediately be noted:

(i) competitive exclusion did not occur in any of the six cages;

(ii) different starting frequencies converged to a common equilibrium zone;

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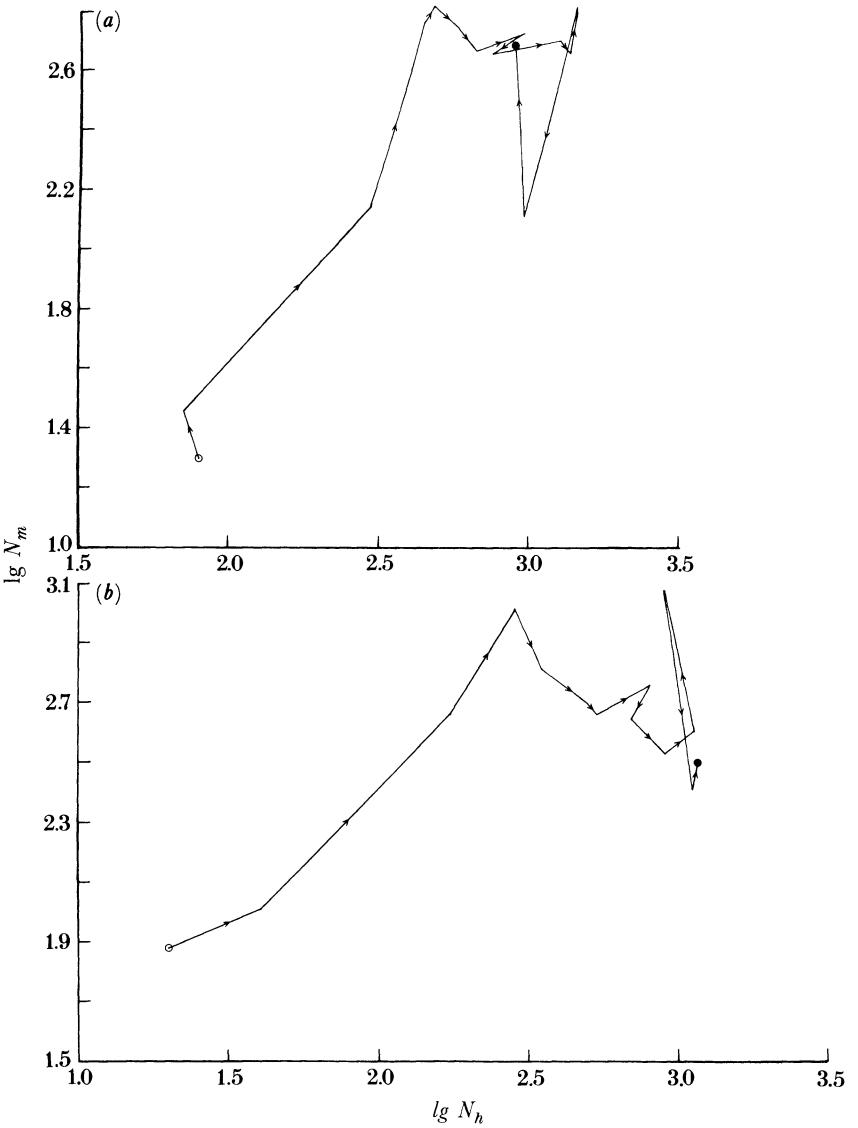

FIGURE 6. Results of experiment HM5: phase plane diagrams. (*a*) Cages started with 20% *D. melanogaster*; (*b*) cages started with 80% *D. melanogaster*.

(iii) there is a good deal of 'noise' in that zone, which makes it difficult to tell whether the equilibrium is a point or a cycle.

As regards the mechanism producing the equilibrium, the first possibility considered was that there might be within-cage but between-bottle resource partitioning. Specifically, cages were always oriented in relation to the incubator light source as shown in figure 9. This means that strongly photopositive flies aggregate at the side of the cage facing the light source. *D. hydei* is indeed strongly photopositive while *D. melanogaster w* is not, the difference between the two being very highly significant (Arthur, unpublished data). Thus it seemed possible that *D. hydei* eggs, and hence larvae, would be aggregated in the three light-side resource bottles. This general sort of situation has been modelled by Atkinson & Shorrocks (1981) and an equilibrium is predicted.

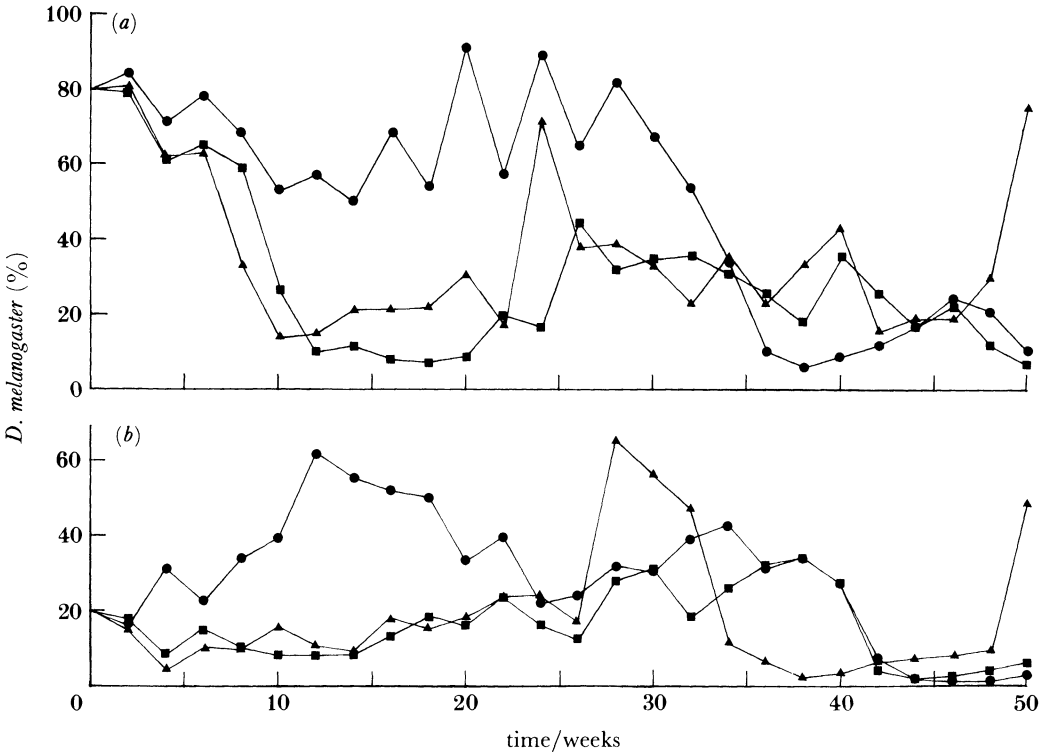

FIGURE 7. Results of experiment HM2L, plotted as species-frequency against time. (*a*) Cages started with 80% *D. melanogaster*; (*b*) cages started with 20% *D. melanogaster*.

Two types of observation made it clear that this was not the stabilizing mechanism. First, no consistent difference could be detected between the frequencies of *D. hydei* in flies emerging from the light-side and dark-side bottles. Second, on repeating the competition experiment in total darkness, the equilibrium remained (experiment HM2D; figures 10 and 11). Thus between-bottle partitioning induced by lighting differences was eliminated as a possible cause of the observed coexistence.

The second possibility considered was within-bottle partitioning through differences in larval feeding depths. This has already been shown to be the cause of stable coexistence in competition between *D. hydei* and the Kaduna strain of *D. melanogaster* (Arthur & Middlecote 1984*b*). To examine whether *D. melanogaster w* and *D. hydei* also differed significantly in larval depth distributions, a single-generation vial experiment was set up as follows. Fifty first-instar larvae of one or other species were placed on the surface of the food-medium in each of a series of vials. Each vial contained a 1.5 cm depth of medium, which is similar to the depth in the 2.5 g resource-bottles. Six replicate vials were set up for each species. To assess distributions of feeding larvae after they had burrowed into the medium but before they returned to the surface to pupate, the medium was sectioned into disks 0.5 cm deep and the number of larvae in each disk counted. Counts were made on days 3 and 4 for *D. melanogaster*, and on days 4 and 5 for the slower-developing *D. hydei*. The results are given in tables 3 and 4. It can readily be seen that *D. hydei* larvae feed, on average, at a greater depth than larvae of *D. melanogaster*. The difference between the two species gives a contingency χ^2 value of 215.6 ($p \ll 0.001$), though some caution is needed in interpreting this because there is heterogeneity between vials within *D. hydei*.

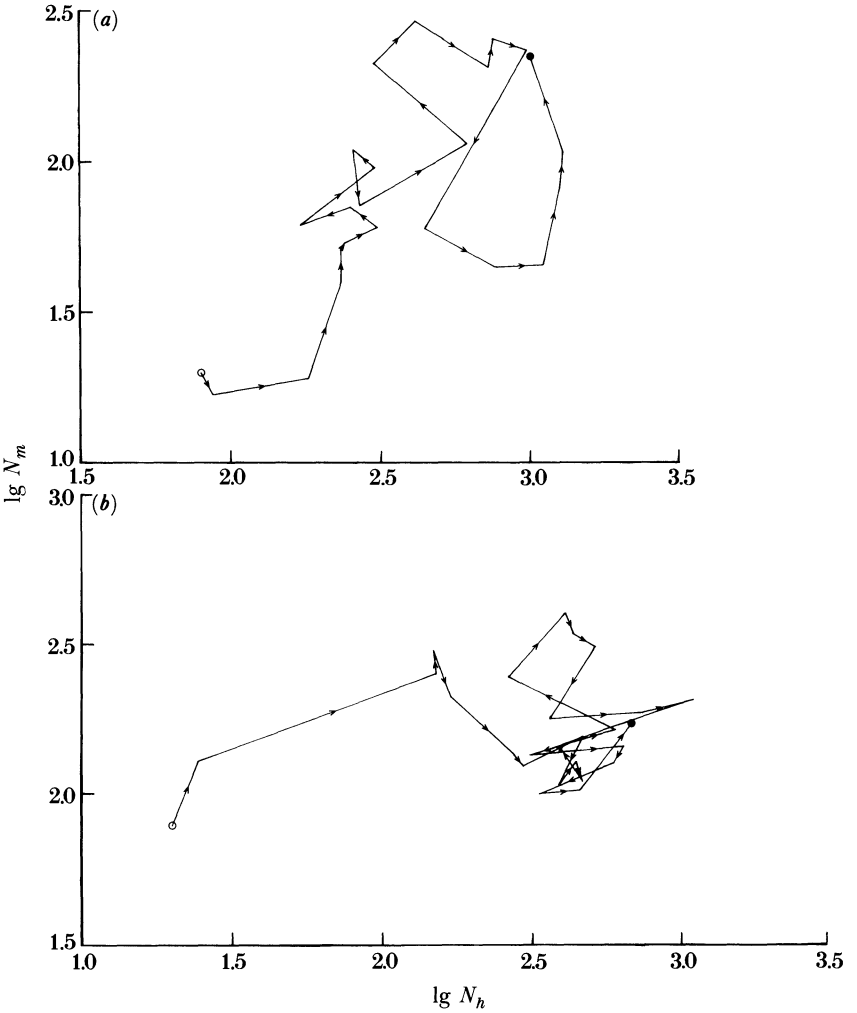

FIGURE 8. Results of experiment HM2L: phase plane diagrams. (*a*) Cages started with 20% *D. melanogaster*; (*b*) cages started with 80% *D. melanogaster*.

Ideally, to show that a particular form of resource partitioning is the cause of a particular stable equilibrium, it is desirable to do three things in addition to demonstrating that competition is actually occurring:

(1) to quantify both species' resource utilization functions along the resource dimension in which the proposed partitioning is suspected, to confirm its existence and reveal its extent;

(2) to show that in environments permitting this form of partitioning stable coexistence does indeed ensue;

(3) to show that in environments preventing this form of partitioning the equilibrium collapses and competitive exclusion results.

In the earlier series of experiments on competition between *D. hydei* and *D. melanogaster* Kaduna (Arthur & Middlecote 1984*b*), it was possible to show these three things, the environment preventing resource partitioning being simply one with a very shallow disk of resource (1.5 g IDM, giving a depth of 0.8 cm). However, in the experiments involving *D. melanogaster w* reported herein, an unexpected complexity arose, which precluded a

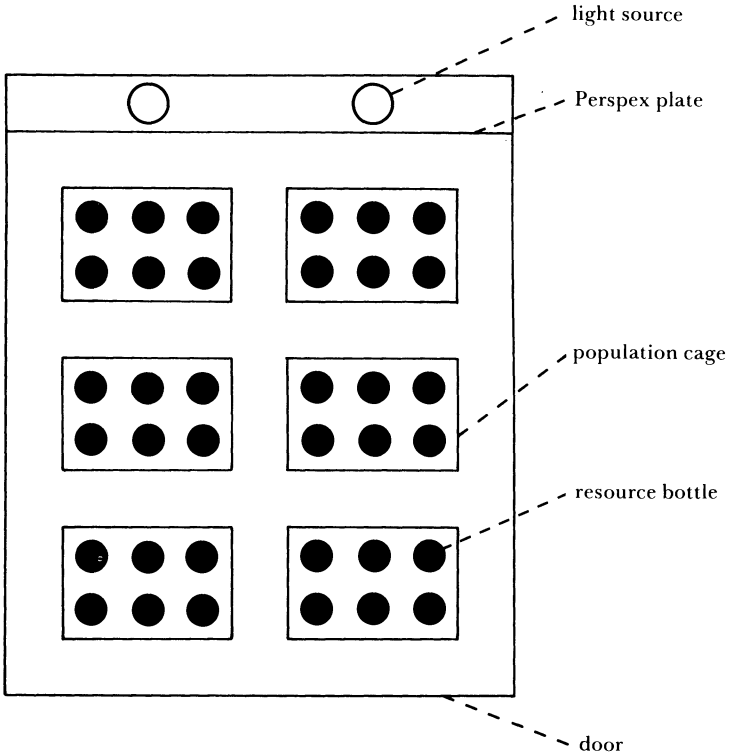

FIGURE 9. Arrangement of population cages on incubator shelf. Cages were always positioned 'broadside on' to the light source.

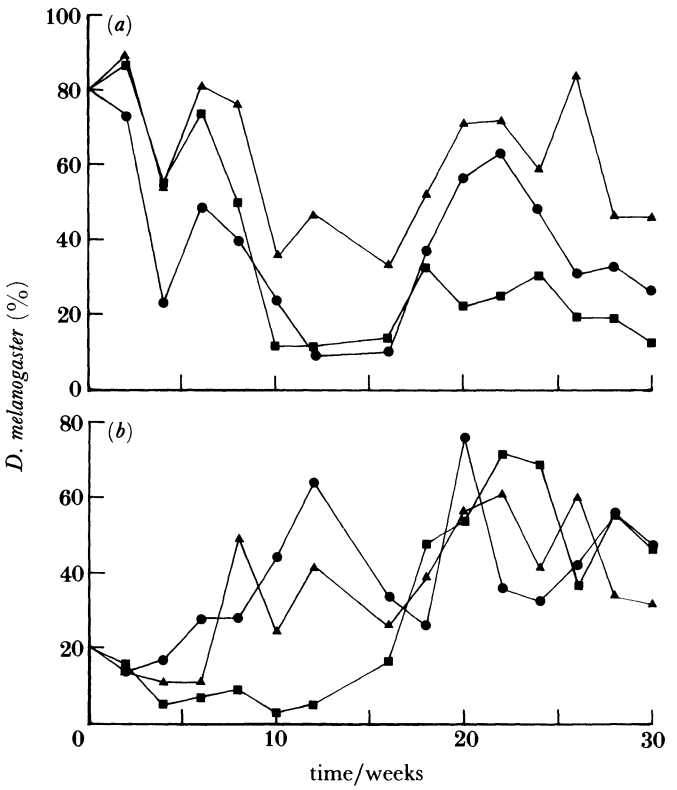

FIGURE 10. Results of experiment HM2D, plotted as species-frequency against time. (*a*) Cages started with l with 80% *D. melanogaster*; (*b*) cages started with 20% *D. melanogaster*.

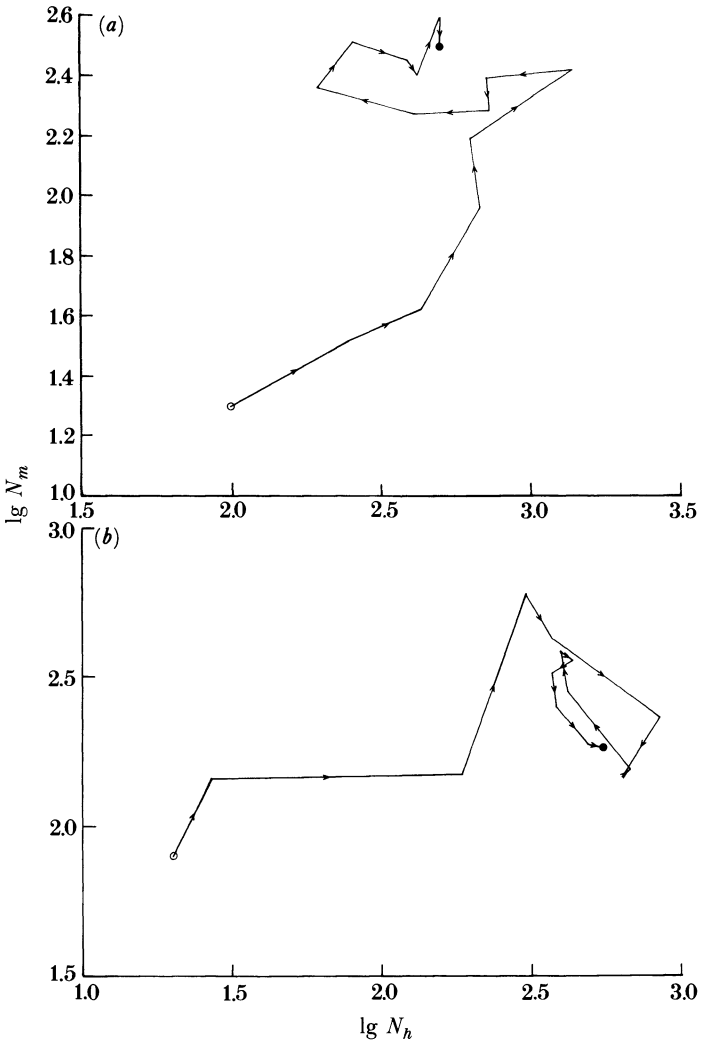

FIGURE 11. Results of experiment HM2D: phase plane diagrams. (*a*) Cages started with 20% *D. melanogaster*; (*b*) cages started with 80% *D. melanogaster*.

TABLE 3. LARVAL DEPTH DISTRIBUTIONS: *D. MELANOGASTER*

day	vial no.	top*	middle	bottom	total
3	1	39	5	0	44
	2	29	10	2	41
	3	35	5	2	42
	total	103	20	4	127
4	1	35	2	0	37
	2	31	2	0	33
	3	36	10	0	46
	total	102	14	0	116
3 and 4	overall	**205**	**34**	**4**	**243**

* Top, middle and bottom refer to the three disks 0.5 cm deep that the overall cylinder of medium (1.5 cm deep) was divided into.

TABLE 4. LARVAL DEPTH DISTRIBUTIONS: *D. HYDEI*

day	vial no.	top	middle	bottom	total
4	1	3	20	25	48
	2	12	17	19	48
	3	19	18	13	50
	total	34	55	57	146
5	1	7	35	7	49
	2	11	20	17	48
	3	10	26	11	47
	total	28	81	35	144
4 and 5	overall	**62**	**136**	**92**	**290**

comparable demonstration of competitive exclusion in a shallow-resource environment. While this preclusion is in some respects regrettable, the reason it occurred is of considerable interest and is described in the next section.

5. STABLE COEXISTENCE WITHOUT RESOURCE PARTITIONING

5.1. *The* 1.5 g *resource experiment*

A further long-term competition experiment was done, identical in all but one respect to the 5 g experiment and the 'light' 2.5 g experiment. The difference was that the resource bottles contained 1.5 g of IDM, giving a depth of only 0.8 cm. As noted above, competition between *D. hydei* and *D. melanogaster* Kaduna in this system results in competitive exclusion (Arthur & Middlecote 1984*b*). However, when *D. hydei* competes with *D. melanogaster w*, a very different outcome is obtained (see figures 12 and 13).

The results exhibit the same three features as those of the 2.5 g experiments, namely:

(*a*) lack of competitive exclusions;

(*b*) convergence of different starting frequencies; and

(*c*) 'noise' in the equilibrium zone, making it difficult to distinguish between a stable point and a cycle.

In relation to this last point, there is a much stronger suggestion of long-term cycle of equilibrium frequencies. However, it is still just a suggestion, and further work would be necessary to confirm or reject this possibility.

5.2. *Apparent lack of resource partitioning*

Despite the uncertainty over the precise nature of the equilibrium, it is clear that an equilibrium of some sort exists, and the key question is what mechanism underlies it. One possibility that obviously needs to be considered is whether resource partitioning – either by depth, or by some other means – is the stabilizing mechanism, as it was in the 2.5 g experiment.

Partitioning by depth?

Depth distributions in the 2.5 g experiment were quantified by setting up vials with comparable depths of resource (1.5 cm), sectioning the medium into disks 0.5 cm deep, and counting the number of larvae in each. The thickness 0.5 cm was chosen because it represents the shallowest disk that can be fairly reliably separated, with its constituent larvae, from the medium beneath it. This means that it is impossible to section the medium in a 1.5 g bottle,

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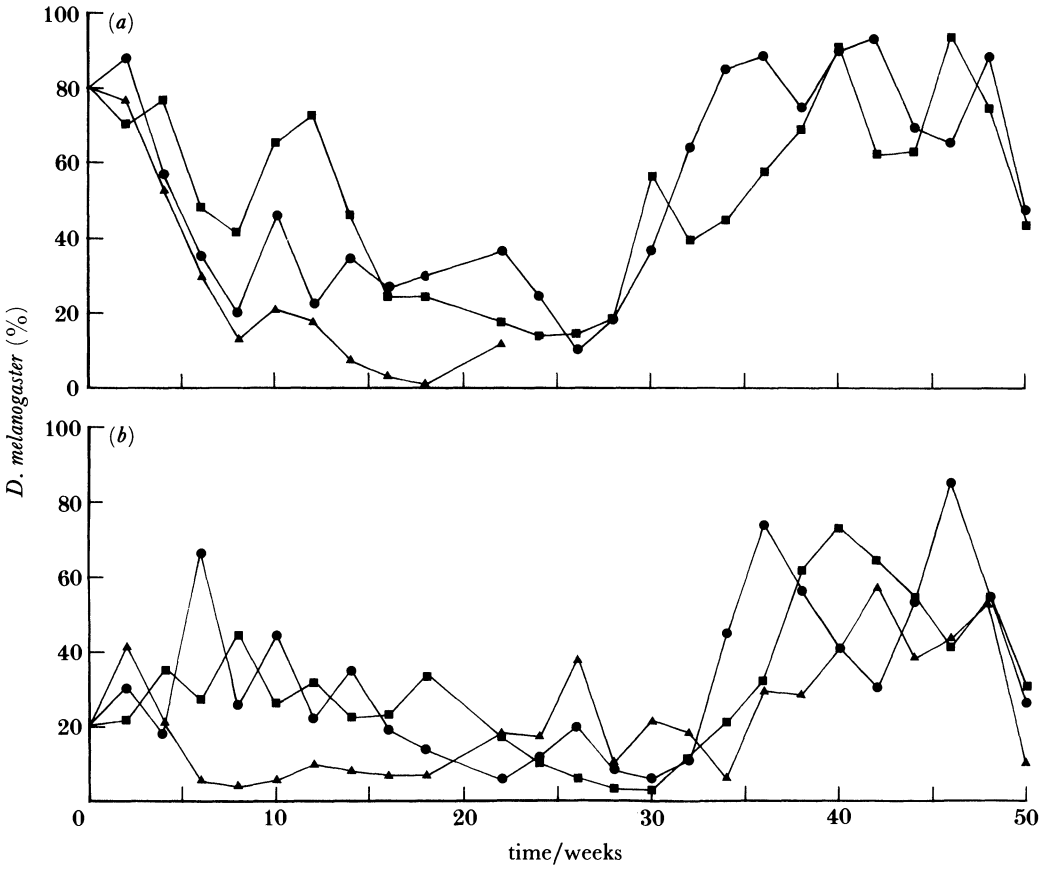

FIGURE 12. Results of experiment HM1, plotted as species-frequency against time. (*a*) Cages started with 80% *D. melanogaster*; (*b*) cages started with 20% *D. melanogaster*.

or its vial equivalent, because the starting depth is only about 0.8 cm, and the medium surface falls as the food is consumed, so that after a few days a 1.5 g bottle contains less than a 0.5 cm depth of resource, and indeed within a fortnight the resource has entirely disappeared.

Although it is impossible to investigate depth distribution because of the shallowness of the medium, it seems most unlikely that significant partitioning by depth occurs in the 1.5 g bottles. Second and third instar larvae of these species can reach lengths of 0.5 cm (*D. hydei* larvae being larger than those of *D. melanogaster*), and tend to feed in an approximately vertical position; thus partitioning by depth is essentially precluded.

Core–periphery partitioning?

Another form of partitioning would occur if one species burrowed into the medium in the centre of the bottle, the other moving out to the periphery before going down to feed. This possibility was examined by taking the central core out of a number of bottles from mixed-species cultures and looking at the number of flies of each species emerging from these cores and from the remaining peripheral regions of medium. The results are given in table 5, and it can be seen that there was no significant partitioning of this sort.

Between-bottle partitioning?

As noted in §4.3, tests of this form of partitioning have proved negative.

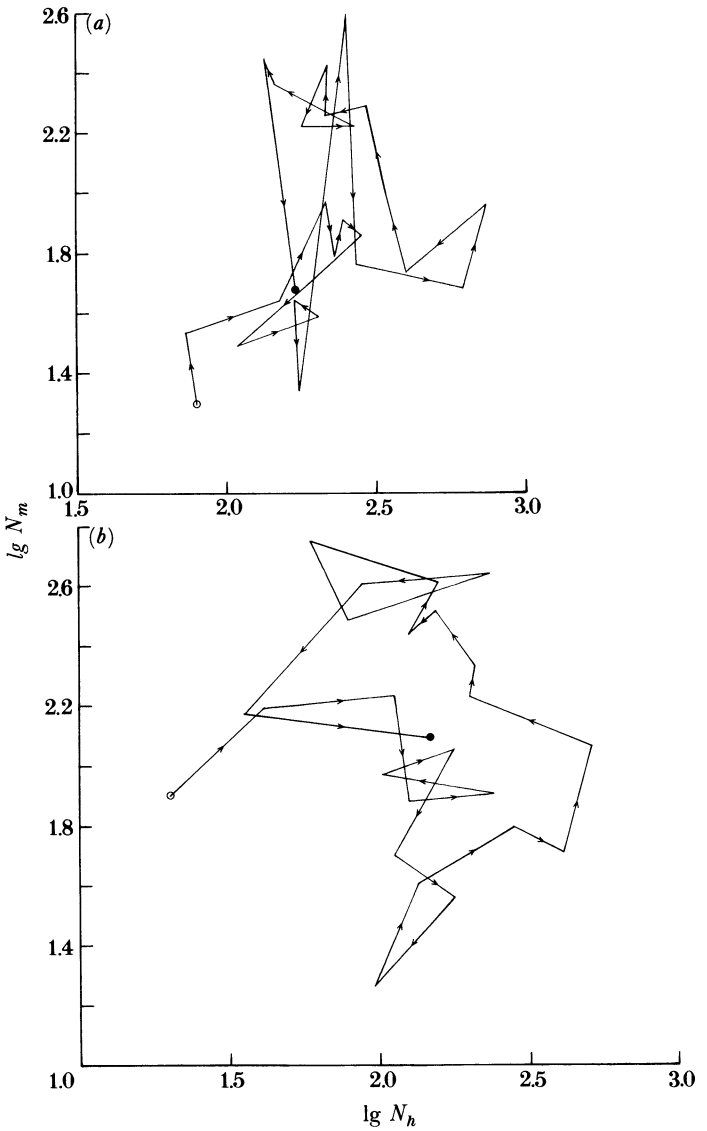

FIGURE 13. Results of experiment HM1: phase plane diagrams. (*a*) Cages started with 20% *D. melanogaster*; (*b*) cages started with 80% *D. melanogaster*.

Temporal partitioning?

In general, temporal partitioning has not been thought to be important as a stabilizing mechanism in interspecific competition (see Schoener 1974). There is a good reason for this in that the conditions under which a temporal difference in resource use will promote stable coexistence are much more restrictive than for the spatial equivalent. Specifically, food removed by the earlier species is no longer available to the later species and this form of 'partitioning' is hence *de*stabilizing unless resource regeneration is very rapid. In the present experiments with *Drosophila* there is *no* within-bottle regeneration and so the fact that, on average, *D. melanogaster* larvae complete their feeding and pupate slightly sooner than *D. hydei* can hardly explain the coexistence.

Table 5. Number of flies emerging from core and periphery of medium

species	replicate	number of flies: core*	number of flies: periphery	number of flies: total	percentage from core
mel	1	298	497	795	37.5
	2	351	341	692	50.7
	3	287	267	554	51.8
	4	275	344	619	44.4
	5	427	248	675	63.3
	6	294	142	436	67.4
	total	**1932**	**1839**	**3771**	**51.2**
hyd	1	132	72	204	64.7
	2	107	61	168	63.7
	3	7	37	44	15.9
	4	99	103	202	49.0
	5	44	94	138	31.9
	6	65	134	199	32.7
	total	**454**	**501**	**955**	**47.5**

* A vial was used to take the core section out of the (wider) bottles. The peripheral medium was left in place. The amounts of medium in 'core' and 'peripheral' categories were approximately equal.

Nutritional partitioning?

Larvae feeding at the same place and time may still partition resources if different resource *types* are present. Indeed, this is the 'classical' mode of partitioning, which has been distinguished from feeding-zone partitioning by Pontin (1982), who calls the former specialization and the latter stratification. This distinction will be discussed in more detail in §6.2. The experiments reported here were all 'one-resource' experiments (cf. Arthur 1980*b*) in that only the resource 'instant *Drosophila* medium' was used. However, like all *Drosophila* media, IDM is chemically heterogeneous. The question that arises is whether larvae can specialize on different constituents of IDM. (These include oat flour, soy flour and wheat flour.) It seems likely that the answer is 'no' and that each unit of hydrated IDM is essentially a random sample of its constituents, but the possibility of this kind of resource partitioning cannot be formally excluded.

Lack of resource partitioning?

The foregoing considerations suggest that the stable coexistence of *D. melanogaster w* and *D. hydei* in the 1.5 g experiment is not caused by resource partitioning. It has not been possible to exclude *completely* the possibility of partitioning, and indeed it may never be possible to do so in any experimental system (see Levin 1972). However, the important question is not whether there is absolutely no resource partitioning but rather *whether some other stabilizing mechanism is causing the equilibrium*. Hence it seems more sensible to look for such a mechanism rather than to search for more and more subtle and slight differences in resource use. The alternative stabilizing mechanism is described in §5.3 and 5.4 below.

5.3. *The fate of D. hydei* 1.5 g *monocultures*

The amounts of distilled water used to hydrate the IDM in 5 g, 2.5 g and 1.5 g bottles were approximately 17, 10 and 6 ml respectively. Thus in the 1.5 g experiment just described, each bottle contained 6 ml water. As has been seen, a stable equilibrium with both species present

was arrived at in this experiment. However, in the most directly comparable *D. hydei* monoculture (H2B: bottles with 6 ml water), a rather surprising result was obtained: complete extinction of all replicate *D. hydei* populations in a handful of generations (see figure 14). Thus although *D. hydei* can reach a non-zero equilibrium population density with *D. melanogaster* present, it cannot do so on its own. This is in contrast, of course, to the cultures with 2.5 g and 5 g resource bottles, where *D. hydei* monocultures are perfectly healthy, and is also in contrast to *D. melanogaster*, which can maintain a stable monoculture population in the 1.5 g system (see figure 14).

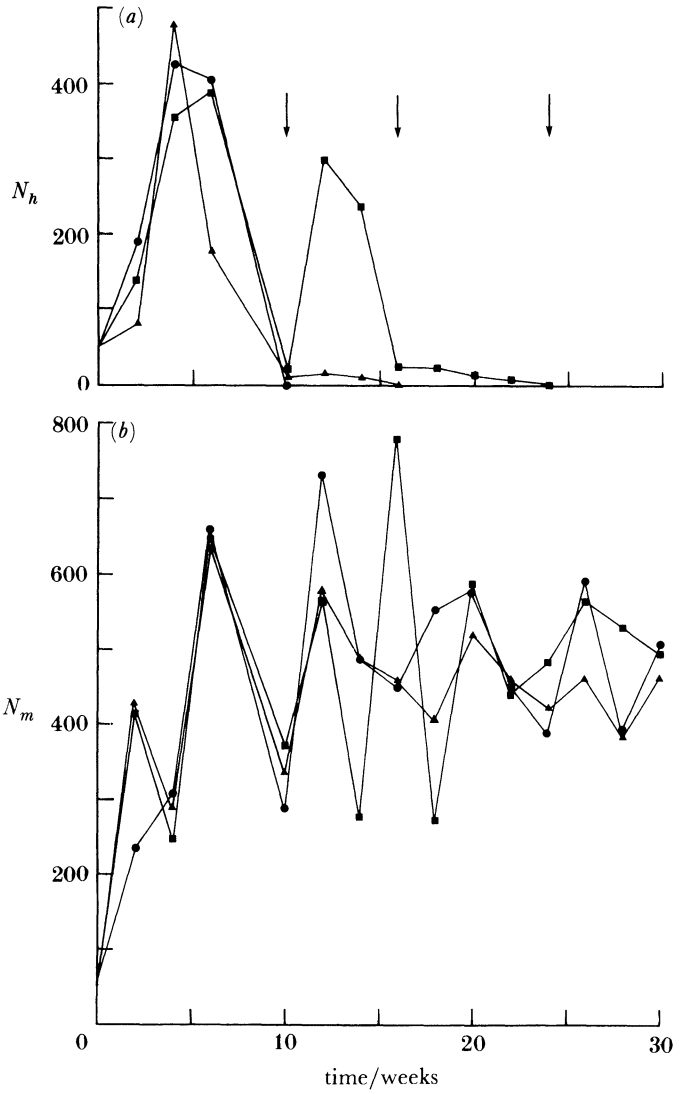

FIGURE 14. Population sizes in monocultures H1B and M1: (*a*) *D. hydei* (H1B); (*b*) *D. melanogaster* (M1). Note that population sizes are given in linear form and for each cage individually. Arrows indicate extinctions.

On close inspection of the state of the medium in the dying *D. hydei* 1.5 g cultures, the source of the problem is readily apparent. In bottles with only 1.5 g of resource, and only *D. hydei* attempting to utilize it, the resource dries up and becomes unusable. Bottles of this kind are shown in figures 15 and 16, plate 2. Interestingly, there are several features of *D. hydei* that

encourage drying out of the medium. One problem is the slower development of this species compared with *D. melanogaster*. Without larval activity, any resource unit will eventually dry out. In the 1.5 g bottles, which are particularly susceptible because of their unfavourable surface area:volume ratio, the resource sometimes dries out before the larvae penetrate it. In this situation, the medium shrinks uniformly around its periphery, detaches itself from the sides of the bottle, and takes the form of a hard, dry 'plug' covered with dead first-instar larvae (figure 15). However, even if larvae penetrate the medium before this happens, and develop as far as second or third instar, the medium may still dry out. This appears to be a consequence of the larger size and greater activity of *D. hydei* larvae, relative to *D. melanogaster*. The high degree of larval activity tends to roll the medium into a ball, detaching it from the glass and giving it more uncovered surface area from which water-loss takes place. Also, the larger *D. hydei* larvae in monoculture leave wider tunnels, which again aid rapid evaporation. (In mixed culture the activities of *D. melanogaster* larvae seem to perforate these wide tunnels and cause them to collapse.) Some cultures die out at a late stage showing the tunnels made by, and the dehydrated remains of, these larvae (figure 16).

Neither the mixed *D. hydei*–*D. melanogaster* 1.5 g cultures nor the *D. melanogaster* monocultures show this marked drying out of the medium. In all cases, the medium in these cultures gradually reduces in depth but remains flat and semi-liquid until shortly before it disappears, at which final stage it does dry out to some extent. Thus it would appear that *D. hydei* survives when *D. melanogaster* is present because of the latter species' supplying the required fluidity of the medium. If this is so, then a *D. hydei* culture with bottles containing 1.5 g resource but extra water should be capable of maintaining a stable population. That this is indeed so can be seen by examining the results of the H1A monoculture, where each bottle had 10.0 ml water (figure 17). A final experiment, in which the amount of water per bottle was reduced to 5.0 ml (H1C, figure 17) showed even more rapid extinction of *D. hydei* monocultures than H1B.

5.4. *Facilitation as the cause of the equilibrium*

What appears to be happening in the 1.5 g mixed culture (experiment HM1) is that if *D. hydei* becomes very common, the medium becomes drier, which favours *D. melanogaster*. However, as *D. melanogaster* increases in frequency the medium becomes more fluid, thus favouring *D. hydei*. That *D. hydei* is indeed the superior competitor in very fluid conditions can be clearly demonstrated in a single-generation competition experiment with 'superfluid medium' (vials with 0.5 g IDM and 3.75 ml water). The results are given in table 6, and it can be seen that the depression in *D. melanogaster*'s numbers in mixed culture is much more drastic than in those of *D. hydei*. Thus we have one-sided (non-mutual) facilitation of *D. hydei* by *D. melanogaster* and a resulting frequency dependence, with each species increasing in frequency when rare, which maintains a state of stable coexistence. It must be stressed that this situation is *not* 'resource partitioning'. The meaning of this term will be discussed in §6.2.

Two problems remain to be discussed. One is essentially terminological (is facilitation compatible with competition?) and is discussed below in §5.5. The other is whether facilitation in relation to water content might be contributing to the equilibrium in the 2.5 g experiments. In fact, this possibility can be completely ruled out. With vials containing the depth-equivalent of 2.5 g or 5 g IDM per bottle, *D. hydei* cultures are much *more* fluid than those of *D. melanogaster*. They are in fact so fluid that in a culture of *D. hydei* 4–5 days old, the medium will run down to the mouth of the vial within minutes of its being laid on its side, in marked contrast to comparable *D. melanogaster* cultures. Thus we have one stabilizing mechanism – resource

FIGURE 15. *D. hydei* monoculture in which the medium dried out before penetration of first-instar larvae.

FIGURE 16. *D. hydei* monoculture that dried out mid-way through the larval period. Note tunnels and dead, dehydrated larvae.

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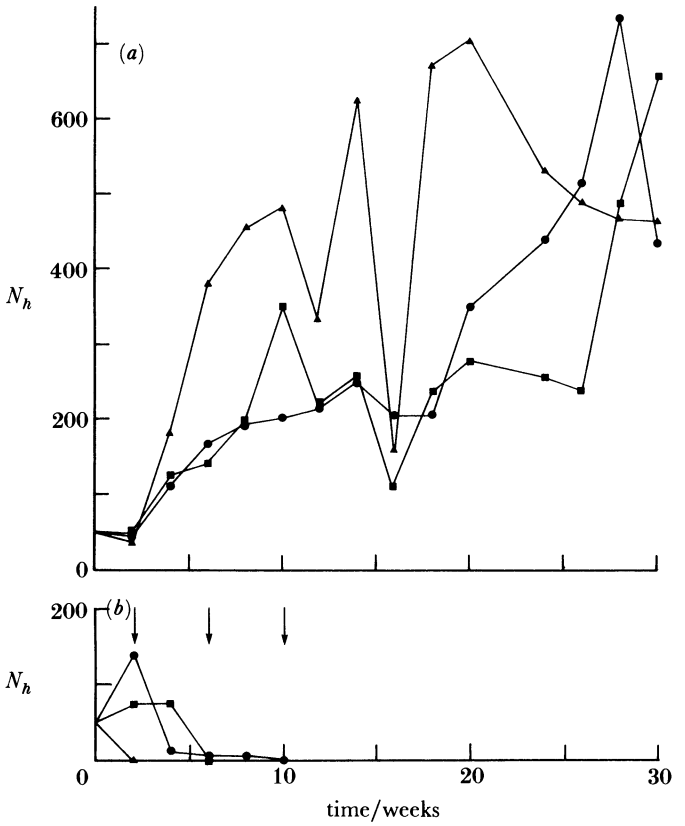

FIGURE 17. Population sizes in monocultures H1A and H1C: (*a*) H1A (10.0 ml water per bottle); (*b*) H1C (5.0 ml water per bottle). Note that population sizes are given in linear form and for each cage individually.

TABLE 6. RESULTS OF COMPETITION IN SUPER-FLUID MEDIUM

replicate no.	no.* of *D. hydei* single	mixed	no.* of *D. melanogaster* single	mixed
1	4	7	77	16
2	5	10	65	15
3	10	16	53	13
4	1	11	49	8
5	5	4	58	7
6	8	11	60	1
7	10	6	74	18
8	19	5	34	9
9	22	8	54	20
10	3	1	89	47
total	**87**	**79**	**613**	**154**
	→		→	
	9.2% reduction		74.9% reduction	

* Number of flies after one generation. Starting numbers were 10♀+10♂ in monocultures and 10♀+10♂ of each species in mixed culture. Parental flies were discarded after 4 days and are therefore not included in the numbers after one generation.

partitioning – that works in 2.5 g cultures but not in 1.5 g ones, and another mechanism – facilitation in relation to water loss – that behaves in a complementary manner. Comparing the phase-plane diagrams of figures 11 and 13 suggests that the facilitation mechanism either takes longer to respond to departures from equilibrium or that its equilibrium is in fact a cycle. However, further experiments will be necessary to test these possibilities.

5.5. *On limiting factors and defining population interactions*

Two ways of defining competition, which are essentially equivalent (see Williamson 1957), are (1) as a (−, −) interaction, and (2) as a situation where two species share a limiting factor. It is of interest to consider whether the interaction occurring between *D. hydei* and *D. melanogaster* in experiment HM1 constitutes competition under either of these definitions, and if not, then which interaction category it falls into. I will take the symbolic definition first.

The individual +'s and −'s that go to make up the symbolic definitions of the various population interactions (+, +), (−, −), etc. can be referred to as facilitation (+) and inhibition (−) when the biological process is anything other than direct energy flow (in which case + = eats and − = being eaten!). Thus competition (−, −) represents mutual inhibition, whereas amensalism (−, 0) is one-way-only inhibition. Mutualism (+, +), in which there is growing interest (see Boucher *et al.* 1982; Vandermeer 1984) is mutual facilitation and has sometimes been referred to as such (Bos *et al.* 1977), whereas commensalism (+, 0) is one-way-only facilitation. (Note that some authors, such as Kenneth (1963) and Maynard Smith (1974), use commensalism to mean (+, +).) 'Neutralism' (0, 0) really means no interaction at all. The only type of two-species interaction for which there is no name (either in Odum (1953) or Williamson (1972) or earlier classifications such as that of Haskell (1947)) except when it occurs as a trophic interaction, is (+, −). This so far unnamed type of

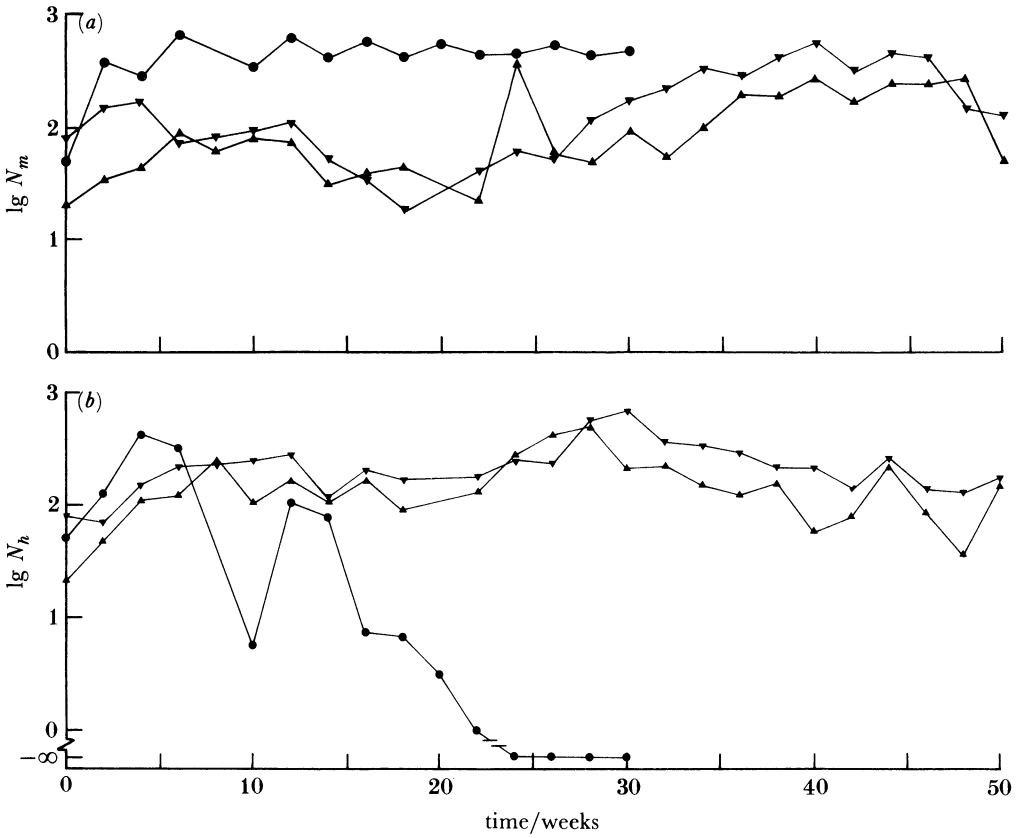

FIGURE 18. Population sizes in the 1.5 g resource system: (*a*) *D. melanogaster*; (*b*) *D. hydei*. ●, Monoculture; ▲, mixed culture (cages started with 20% of the species concerned); ▼, mixed culture (cages started with 80% of the species concerned).

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interaction is exemplified by the *D. melanogaster w*/*D. hydei* 1.5 g system (see table 7 and figure 18). How common this type of interaction is remains to be seen, but since it clearly can occur it needs to have a name. I suggest that it be called *contramensalism* because the two species have opposite effects (hence 'contra') on each other's limiting resource or 'table' (hence 'mensalism', from the Latin *mensa*, as also found in amensalism and commensalism).

Table 7. K, $\hat{N}$, α and β values: 1.5 g system

species	K	$\hat{N}$	effect on other species
D. melanogaster	477	63	-4.13 $(=\beta)$
D. hydei	0	260	$+1.59$ $(=\alpha)$

It is appropriate to turn, at this stage, to the definition of competition in terms of limiting factors and to ask what does indeed limit the populations in the 1.5 g system. Assuming that the explanation of that system given in the preceding section is correct, the two populations in experiment HM1 have different limiting factors. *D. hydei* increases (at the expense of *D. melanogaster*) until conditions become too dry for it, whereupon it encounters its limit and begins to decline. At this stage *D. melanogaster* begins to increase, and does so until the damper conditions it creates cause *D. hydei* to increase again and usurp the food supply. Thus *D. melanogaster* is food-limited and *D. hydei* moisture-limited. Again, as when using the symbolic version of the definition, this system is not classifiable as competition.

Since contramensalism is a potentially stabilizing type of interaction (see further discussion in §6.3), its commonness in natural communities will be of considerable interest. One possibility is that, because its '+' component takes place through modification of the environmental *milieu*, contramensalism might be common in organisms living in close physical association, such as insect larvae, and rare in organisms living separately and merely sharing a common food supply, such as many birds.

A final comment that should be made about contramensalism is that its (+, −) nature is most readily apparent in the comparison of mixed and single-species cultures. In the 1.5 g experimental system, addition of *D. hydei* to a *D. melanogaster* monoculture has a negative (−) effect on the *D. melanogaster*. Addition of *D. melanogaster* to a *D. hydei* monoculture has a positive (+) effect on the *D. hydei* – indeed, without such an addition the *D. hydei* culture will die out, as we have seen. Not all manipulations of density *within* mixed cultures will reveal the essential nature of the interaction. However, the same could be said of some other interaction types, such as amensalism and competition

6. Discussion

The most notable feature of the *Drosophila* experiments reported here is the diversity of causative factors underlying apparently similar results. Specifically, the stable coexistences found in three sets of experiments differing in the amount of resource are brought about in three distinct ways. With 5 g of resource per bottle, the coexistence occurs simply because the environment is favourable to both species and there is no inhibitory effect in either direction between them; that is, neither competition nor amensalism (nor any other type of interaction) takes place. When the amount of resource is reduced by half, strong interspecific competition occurs, the inhibitory effect of *D. hydei* on *D. melanogaster* being approximately twice as great

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as the reverse effect. In this case stable coexistence is again obtained, but now it occurs despite the strong competition and because of an interspecific difference in the depth of larval feeding zones. Finally, when the amount of resource per bottle is reduced to a shallow disk of less than 0.8 cm in depth (1.5 g IDM), to prevent resource partitioning, stable coexistence is again obtained. However, in this case the interaction has shifted from a $(-, -)$ to a $(+, -)$ type, and the observed stable coexistence occurs through yet another distinct mechanism.

The two stabilizing mechanisms revealed here – resource partitioning and facilitation – will be discussed further in §6.2 and 6.3 respectively, while the general message that the whole series of experiments conveys for competition theory will be examined in §6.4. First, though, I shall briefly discuss the relation between the results presented in this paper and other results on the ecological interaction between *D. hydei* and *D. melanogaster*.

6.1. *Interactions between D. hydei and D. melanogaster*

Apart from a brief note (Miller 1954) suggesting that a state of coexistence of these two species might be caused by specialization on food-units of different ages, which has not been confirmed, the only published experimental work on ecological interactions between *D. hydei* and *D. melanogaster* appears to be that originating from my own laboratory. Previous work took the form of an analysis of the mechanism of coexistence in competition between *D. hydei* and the wild-type Kaduna strain of *D. melanogaster* (Arthur & Middlecote 1984*b*), and an investigation of an evolutionary change in *D. hydei* that destabilized a state of coexistence involving that species and *D. melanogaster w* (Arthur & Middlecote 1984*a*). The question that now arises is how these two earlier studies and the present one fit together.

As regards the mechanism of coexistence, the *D. hydei*–*D. melanogaster w* system and the *D. hydei*–*D. melanogaster* Kaduna system exhibit interesting differences, which are summarized in table 8. Basically, all the differences are explicable in terms of the increased competitive ability and general fitness of the Kaduna stock compared with the mutant one. The *w* mutation not only produces a white eye colour and various other effects on pigmentation (see Lindsley &

TABLE 8. COMPARISON OF RESULTS OF INTERACTION BETWEEN (1) *D. HYDEI* AND *D. MELANOGASTER* KADUNA AND (2) *D. HYDEI* AND *D. MELANOGASTER W*

strain of *D. melanogaster*	resource level (g)	type of interaction	result[1]	stabilizing mechanism	source
Kaduna	5.0	$(-,-)$[2]	cx	partitioning	Arthur & Middlecote (1984*b*)
	2.5[3]				
	1.5	$(-,-)$[2]	ce	none[4]	
white-eye	5.0	(0,0)	cx	independence[5]	this paper
	2.5	$(-,-)$	cx	partitioning	
	1.5	$(+,-)$	cx	facilitation	

Notes:
1. cx, Stable coexistence; ce, competitive exclusion.
2. Inferred from data deriving from vial experiments.
3. No results have been published for this experiment. It has been conducted once with unclear results and needs to be repeated.
4. None means 'none sufficient to produce an equilibrium'.
5. The populations coexisted in this system simply because they did not interact: i.e. the populations were effectively independent despite being sympatric.

Grell 1968), but also a generally lengthened developmental period, with flies taking longer to reach any particular stage of the life-cycle than their wild-type equivalents. Experiments on the particular *w* stock used here indicated that the mean generation time was lengthened by about one day compared with Kaduna. The effects of replacing the white-eyed stock with Kaduna in the two-species long-term experiments are as follows. First, it appears that there *is* a competitive interaction in 5 g resource systems and that the stable coexistence therein is caused by depthwise resource partitioning (quantified in Arthur & Middlecote 1984*b*). That is, the *D. hydei–D. melanogaster* K 5 g system is very similar to the *D. hydei–D. melanogaster w* 2.5 g system. Second, in the 1.5 g system, where depthwise resource partitioning is precluded by the shallowness of the resource, *D. melanogaster* K rapidly eliminates *D. hydei*. However, some care is required in interpreting this result. It almost certainly is a genuine competitive exclusion rather than an extinction of *D. hydei* owing to drying of the medium. Although equivalent *D. hydei* monocultures go extinct because of this problem of dryness, the medium in 1.5 g mixed cultures is extremely fluid. It would appear that *D. melanogaster* K renders the medium suitable for *D. hydei* by liquefying it (as does *D. melanogaster w*), but then proceeds to out-compete *D. hydei*. That is, the causes of extinction of *D. hydei* in monoculture and in mixed culture are different.

Turning to the evolutionary change that occurred in some populations of *D. hydei* (Arthur & Middlecote 1984*a*), the data on that phenomenon were obtained from a two-species system similar to the one used here (i.e. involving *D. melanogaster w*, not Kaduna). However, they are actually *less* easy to connect with the present results than were the data on the *D. hydei–D. melanogaster* K system. The evolutionary change that took place in *D. hydei* was towards pupation in the cages rather than the resource bottles. This happened in cages in which *D. hydei* was originally coexisting with *D. melanogaster w*, but after the change *D. melanogaster* was competitively excluded. The problem is that the present results show that in 5 g resource systems, *D. hydei* and *D. melanogaster w* do not actually compete. Thus, rather than the evolutionary change in *D. hydei* being a *response* to competition, it must have actually *caused* competition as well as competitive exclusion. Whereas it is clear why the evolutionary shift in pupation site would give *D. hydei* an advantage, and could thus lead it to exclude *D. melanogaster w* competitively (see Arthur & Middlecote (1984*a*) for details), it is not clear why it should also have caused a switch from a non-competitive to a competitive situation. This problem requires further study.

6.2. *What is resource partitioning?*

The literature on competition, including earlier sections of this paper, is strewn with references to resource partitioning. One might therefore suppose that population biologists have a precise meaning for this term. However, this seems not to be so, and several problems in this area deserve mention. First, it is desirable to distinguish *resource partitioning* (which, despite its name, usually implies only partial non-overlap in utilization curves) both from *resource identity* (coincident utilization curves) and from *resource segregation* (completely non-overlapping curves). Second, we should acknowledge that if we depart from the idealized situation of normally distributed resource utilization functions, other possibilities exist, such as curves with coincident ranges but opposite skews. It seems reasonable to consider these to constitute a form of resource partitioning, but this is a fundamentally different situation from that of two partly overlapping normal distributions, where each species has a *unique* section of resource spectrum (a 'food

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refuge'). Finally, if partitioning occurs in more than one dimension, further problems arise (see Pianka 1981).

While resource identity featured in some (unhelpful) versions of the competitive exclusion principle, it is unlikely ever to be found in nature or, for that matter, in the laboratory. In contrast, resource partitioning and resource segregation are both common. Although resource segregation in any particular dimension implies lack of competition, resource partitioning (or even identity) does not imply that there *is* competition – both because other dimensions may show segregation and because resources may not be limiting. In this context, it is worth mentioning that the *D. hydei–D. melanogaster w* 5 g system exhibits resource partitioning rather than resource segregation in terms of larval depth distributions, but also a lack of competition.

Turning to the nature of the *x*-axis of a standard resource utilization curve, we encounter further difficulties. If it is a chemical variable, such as water content of seeds eaten by a pair of consumer species, or a physical variable, such as the size of those seeds, then partly overlapping utilization curves clearly constitutes resource partitioning. Pontin (1982) describes this situation as *specialization*. If the *x*-axis is a spatial variable such as vertical distance, which applies to the 2.5 g *Drosophila* system described herein and probably also to Gause's (1935) *Paramecium* experiments, then partly overlapping utilization curves are again describable as resource partitioning, though Pontin (1982) describes this situation as *stratification*. However, if we turn through 90° and consider partly overlapping utilization curves in horizontal space, this situation is usually *contrasted* with resource partitioning, especially if the horizontal space concerned is in patches rather than a continuum. Whether it is sensible to stress this contrast is debatable.

The main message I wish to get across here is that the distinction between the first two types of stabilizing mechanism given in the Introduction–resource partitioning and spatial aggregation–is not at all clear-cut. All situations in which the limiting resource, whether internally homogeneous or heterogeneous, undergoes differential use by competing species can be described as resource partitioning; all give rise to frequency-dependent competitive abilities and thereby, in some cases, to stable coexistence. A classification of resource partitioning in the broadest sense is given in figure 19. Needless to say, the different kinds of partitioning shown in the figure are not all mutually exclusive.

It is instructive to consider the possible reasons for differential aggregation of two (or more) species over a series of patches as proposed by Shorrocks *et al.* (1979; see also Atkinson & Shorrocks 1981). These authors assume nutritionally homogeneous patches, so differential aggregation cannot result from a species choosing a patch for nutritional reasons. This leaves two possibilities: first, differential aggregation due to variation in some factor extrinsic to the resource, e.g. some patches more brightly lit than others; and second, differential aggregation as a result of chance arrival of ovipositing females of the two species in different patches (see Atkinson & Shorrocks 1984). The first of these two situations is similar to the *D. hydei–D. melanogaster* difference in larval depth distributions in that both involve *repeatable* differences between the species. However, differential aggregation by chance arrival is a fundamentally different process, since it is *not* repeatable. Here, different replicates of a system of patches might all give rise to differential aggregation, but the exact patches utilized by one particular species would differ from one replicate to the next.

This difference between repeatable and non-repeatable patterns of differential resource use is in some ways more fundamental than the difference in dimension (horizontal against

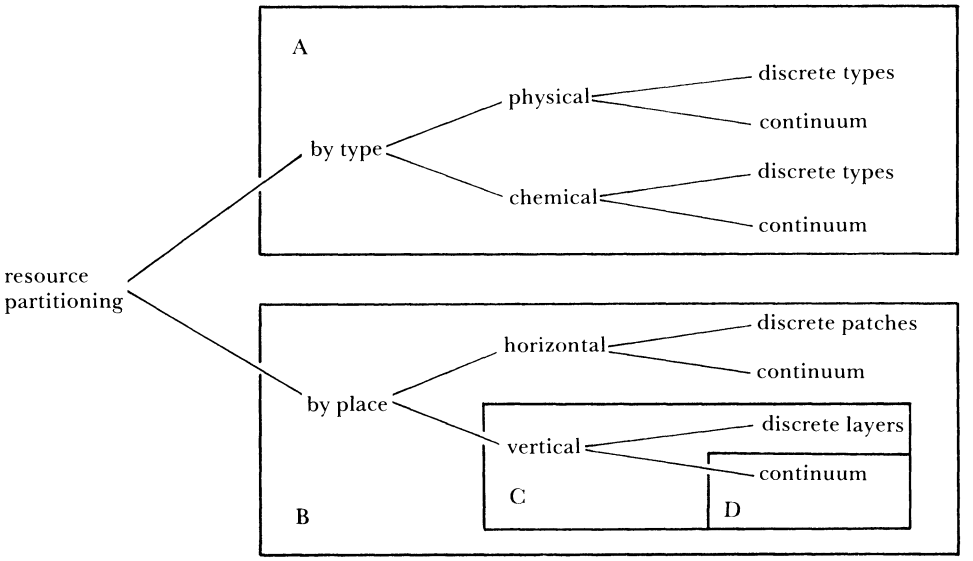

FIGURE 19. Types of resource partitioning. A represents 'specialization'. B represents the broadest possible interpretation of 'stratification', while C represents a narrower and more literal interpretation. D includes the 2.5 g *Drosophila* system reported here, the 5 g *Drosophila* system of Arthur & Middlecote (1984*b*), and probably also the *P. aurelia–P. bursaria* and *P. caudatum–P. bursaria* systems of Gause (1935). See text for further explanation.

vertical) or the difference between discrete and intergrading resource units (patches against layers). It could be argued that since patches of resource in nature will almost always exhibit some slight differences in intrinsic (nutritional) and/or extrinsic factors, the non-repeatable form of differential aggregation based *entirely* on chance effects is unlikely to be common. This is not to say, of course, that chance has no effect at all on the actual distribution patterns that develop in any particular case. A combination of chance effects and variation in intrinsic and extrinsic features of resource units seems the most likely situation in nature.

One final coment is necessary on the meaning of resource partitioning. Situations where the environment 'cycles', favouring first one species then the other, such as the *D. hydei–D. melanogaster w* 1.5 g system, do *not* constitute resource partitioning in the normal sense of the term. Partitioning occurs when a range of resources is present at any one time and the species exhibit differential *choice* of those resources. The concept of 'temporal resource partitioning', which tends to obscure the difference between these two situations, is usually ill-thought-out, is unlikely to be an important cause of coexistence (see Schoener 1974) and is best dropped altogether from the ecological vocabulary. The key question in systems with a cyclically varying resource is whether the cycling is caused by the species themselves. It is only when this is the case that the system is likely to be frequency-dependent and hence to give rise to stable coexistence.

6.3. *Contramensalism*

Although resource partitioning was responsible for the state of coexistence in the 2.5 g experiments, we have seen that the coexistence in the 1.5 g system was balanced in a different way. Basically, the balance arose out of the nature of the interaction itself. That is, it is *because* the interaction was of a (+, −) nature – of the sort that I have called contramensalism – that the system is stable. The question that now arises is whether contramensalism automatically produces coexistence. Actually, it does not, and the obtaining of coexistence in the 1.5 g system

used was dependent on a particular state of affairs that can be illustrated as in figure 20: the left-hand diagram shows a schematic interpretation of the *D. hydei–D. melanogaster w* 1.5 g system, and the right-hand diagram illustrates an alternative (hypothetical) experiment where contramensalism does not produce an equilibrium. However, it is clear that cases of contramensalism not leading to equilibrium will often still lead to frequency dependence (as in figure 20*b*). Thus contramensalism will constitute a potential stabilizing mechanism in a wider range of conditions than those under which it produces an actual equilibrium. Also, as with the competitive stabilizing mechanisms listed in the Introduction, contramensalism is potentially applicable to interactions between genotypes as well as to interactions between species.

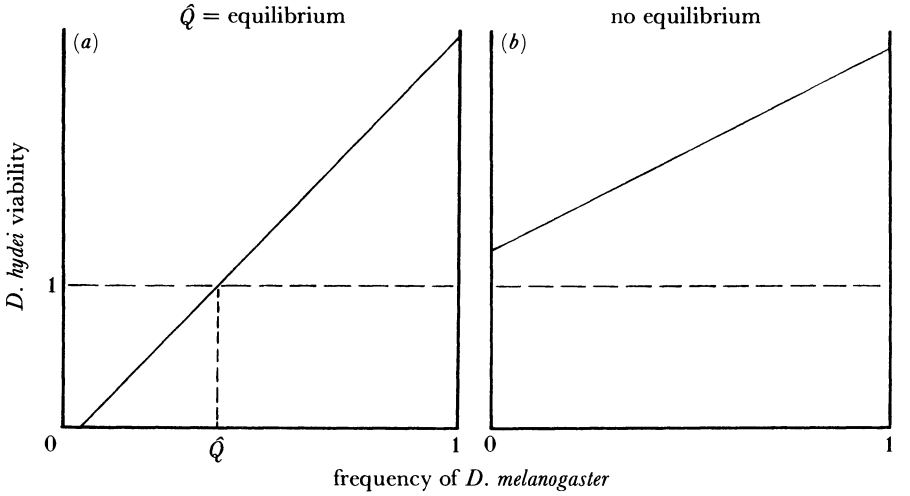

FIGURE 20. The stabilizing effect of contramensalism: (*a*) interpretation of the 1.5 g resource system results; (*b*) results of a hypothetical experiment for comparison. With respect to *D. hydei* viability, 1 means equal to *D. melanogaster*, 0 means non-viable.

Is contramensalism an interesting oddity, or is it likely to be fairly widespread in nature? No answer can yet be given to this question, but two points can be made that relate to it. First, as noted in §5.5, it seems likely that contramensalism is rare among guilds of organisms that only interact in sharing a food source, but possible that it is common in organisms living in close physical association. Second, if contramensalism is viewed as an 'accidental' (as opposed to evolved) effect superimposed on an essentially competitive interaction, it might be reasonable to expect it to be commoner among congeners (and among genotypes) than either of the other interactions involving facilitation – i.e. commensalism and mutualism – where no 'minus' effect remains.

6.4. *Competition theory and the complexity of simple environments*

The experiments reported here reveal the complexity of population processes that can be found even in a simple environment. The systems used were simpler by far than most natural environments in spatial structure, resource composition, and diversity of consumer species. Yet with minor alterations in the amount of resource (and with choice of a different genetic strain of one of the species) the population dynamics of the system changed radically. What relevance, we may now ask, has this complexity of outcome for competition theory?

It would seem that the answer to this question is that the dominant theme of competition

theory – the competitive exclusion principle and the theory of limiting similarity – should be regarded neither as a universally acceptable approach to be totally embraced, nor as a completely unrealistic one to be totally abandoned. Pontin (1982) seems, regrettably, to be taking the latter view when he says that the competitive exclusion principle is 'not worth saying' and that the theory of limiting similarity is an 'unrealistic idea'. Rather, within the group of experiments reported here, some systems appear to be stabilized by resource partitioning and, where it has been possible to test theoretical predictions of limiting similarity for those systems (Arthur & Middlecote 1984*b*), they have been borne out. However, other systems appear not to be stabilized by resource partitioning, and indeed the 1.5 g experiments reported here do not even constitute competition. In such cases, as well as those where it appears that there is *competitive* coexistence caused by mechanisms other than resource partitioning, the idea of limiting similarity is simply not applicable. Thus we need (*a*) several branches of competition theory, each dealing with a particular class of systems delineated on the basis of which competitive stabilizing mechanism is operating; and (*b*) several branches of 'horizontal interaction theory' (as opposed to 'vertical' or 'trophic' interaction theory), of which competition theory is only one, namely the one that deals with truly (−, −) interactions.

Although these conclusions derive from a single series of experiments, it is worth noting that in most cases where interactions involving a pair or group of closely related species have been analysed in detail, the situation has turned out to be complex. There are often aspects of the interaction that do not fit into 'conventional competition theory', and these have been overlooked while the 'resource partitioning' aspects have been overemphasized. This is certainly true of Gause's (1935) work, where processes involving the effect of waste products have been played down, whereas resource partitioning in the form of stratification has been much stressed, despite the lack of any quantitative data showing that it did indeed occur. Perhaps, if 'horizontal interaction theory' itself becomes appropriately complex, we can stop attempting to constrain the diversity of real interactive systems into a single theoretical mould.

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Appendix

The tables below give population sizes in all individual cages of all experiments. The experiment codes (M5, etc.) are explained in table 1 in the text. It should be noted that '0' means $N = 0$ whereas '—' means that no count was made during the week indicated.

Monocultures

D. melanogaster

Experiment M5

week	cage A	cage B	cage C
0	50	50	50
2	171	155	122
4	—	—	—
6	787	1011	1778
8	778	1153	1095
10	822	592	936
12	696	613	808
14	816	528	642
16	578	616	701
18	631	532	439
20	684	393	195
22	495	510	374
24	399	480	288
26	482	478	462
28	395	598	356
30	554	454	486

D. melanogaster

Experiment M2

week	cage A	cage B	cage C
0	50	50	50
2	215	344	213
4	441	712	793
6	578	804	741
8	—	—	—
10	576	602	698
12	743	938	666
14	586	711	677
16	632	704	624
18	389	482	595
20	405	590	508
22	536	798	869
24	511	670	695
26	426	595	770
28	506	288	475
30	398	435	476

D. melanogaster

Experiment M1

week	cage A	cage B	cage C
0	50	50	50
2	238	421	424
4	310	246	290
6	657	656	649
8	—	—	—
10	288	370	340
12	731	568	578
14	488	275	488
16	456	778	460
18	553	272	409
20	581	583	519
22	450	443	457
24	391	480	423
26	584	563	461
28	386	532	385
30	501	497	460

D. hydei

Experiment H5

week	cage A	cage B	cage C
0	50	50	50
2	3	29	42
4	461	188	541
6	—	—	—
8	728	571	3051
10	907	703	2175
12	1019	743	726
14	749	875	2075
16	547	471	1402
18	748	532	1163
20	374	818	696
22	524	617	401
24	618	482	253
26	345	554	223
28	745	633	502
30	467	352	439

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Monocultures (cont.)

D. hydei

Experiment H2

week	cage A	cage B	cage C
0	50	50	50
2	82	142	104
4	321	427	561
6	135	192	573
8	—	—	—
10	342	595	1521
12	88	591	890
14	244	388	1045
16	121	443	701
18	218	90	859
20	429	83	143
22	513	279	488
24	209	164	397
26	210	180	692
28	145	377	1670
30	352	511	68

D. hydei

Experiment H1A

week	cage A	cage B	cage C
0	50	50	50
2	42	44	40
4	116	126	185
6	170	142	383
8	193	194	458
10	203	355	480
12	216	220	339
14	255	262	628
16	206	112	158
18	205	236	674
20	352	280	713
22	—	—	—
24	440	260	533
26	520	239	493
28	740	488	468
30	433	662	461

D. hydei

Experiment H1B

week	cage A	cage B	cage C
0	50	50	50
2	191	138	82
4	428	357	482
6	406	383	178
8	—	—	—
10	0	16	1
12	—	299	14
14	—	237	12
16	—	23	0
18	—	21	—
20	—	10	—
22	—	2	—
24	—	0	—

D. hydei

Experiment H1C

week	cage A	cage B	cage C
0	50	50	50
2	138	73	0
4	9	75	—
6	1	0	—
8	1	—	—
10	0	—	—

Mixed cultures

Experiment HM5*, cages with initial frequency of 20% *D. melanogaster*

	cage A		cage B		cage C	
week	N_{mel}	N_{hyd}	N_{mel}	N_{hyd}	N_{mel}	N_{hyd}
0	20	80	20	80	20	80
2	26	83	18	69	43	62
4	107	335	90	246	226	305
6	536	476	484	468	860	356
8	536	336	600	632	1048	472
10	592	420	444	732	588	564
12	660	380	464	872	256	724
14	1008	436	260	856	284	952
16	700	516	532	884	100	848
18	652	552	648	1012	164	1424
20	687	624	478	1188	163	2196
—	—	—	—	—	—	—
30	907	1025	584	1289	570	2060
—	—	—	—	—	—	—
40	164	389	149	855	81	1585
—	—	—	—	—	—	—
50	1194	772	240	785	29	1131

* In this experiment, population estimates for weeks 6 to 18 inclusive were obtained by dividing the population into four approximately equal-sized groups, counting one of them, and quadrupling.

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Mixed cultures (cont.)

Experiment HM5, cages with initial frequency of 80% *D. melanogaster*

	cage A		cage B		cage C	
week	N_{mel}	N_{hyd}	N_{mel}	N_{hyd}	N_{mel}	N_{hyd}
0	80	20	80	20	80	20
2	37	25	172	30	101	68
4	344	150	599	162	462	211
6	948	200	1088	248	1036	404
8	792	256	556	376	584	404
10	864	304	272	476	356	680
12	844	256	172	672	360	652
14	888	412	148	932	680	1020
16	376	404	124	672	844	988
18	424	528	116	972	484	1144
20	464	558	168	1202	579	1581
—	—	—	—	—	—	—
30	1132	876	1636	1038	836	743
—	—	—	—	—	—	—
40	495	521	122	1106	170	1697
—	—	—	—	—	—	—
50	834	701	57	1383	67	1334

Experiment HM2L, cages with initial frequency of 20% *D. melanogaster*

	cage A		cage B		cage C	
week	N_{mel}	N_{hyd}	N_{mel}	N_{hyd}	N_{mel}	N_{hyd}
0	20	80	20	80	20	80
2	14	80	18	94	19	85
4	7	156	20	45	31	349
6	29	271	39	141	53	291
8	36	345	99	193	19	162
10	42	233	92	146	28	337
12	43	341	93	58	45	527
14	43	450	151	125	16	177
16	63	284	98	91	21	139
18	57	321	242	245	84	347
20	60	279	168	340	58	295
22	109	351	163	245	55	179
24	73	236	92	330	46	242
26	177	877	71	226	97	730
28	321	170	129	276	186	469
30	499	388	227	525	156	341
32	358	405	263	416	159	722
34	112	887	109	147	393	1121
36	42	691	293	652	441	940
38	41	1610	282	554	382	739
40	31	935	84	226	64	173
42	71	1055	38	527	27	715
44	108	1546	11	520	19	1231
46	196	1301	9	1142	41	1346
48	264	1091	25	1964	32	836
50	551	564	30	1113	84	1333

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Mixed cultures (cont.)

Experiment HM2L, cages with initial frequency of 80% *D. melanogaster*

	cage A		cage B		cage C	
week	N_{mel}	N_{hyd}	N_{mel}	N_{hyd}	N_{mel}	N_{hyd}
0	80	20	80	20	80	20
2	186	43	96	18	105	28
4	321	202	123	50	309	198
6	255	151	246	70	404	219
8	96	198	208	96	317	220
10	42	262	231	206	132	360
12	55	310	270	201	42	364
14	63	233	292	292	113	868
16	45	170	216	96	77	925
18	75	265	238	200	62	881
20	38	84	165	16	128	1309
22	40	195	196	148	195	834
24	44	23	86	10	363	1776
26	97	159	251	139	391	483
28	152	233	621	135	408	866
30	114	230	431	211	479	875
32	120	396	334	294	477	847
34	166	301	126	245	242	532
36	231	767	77	726	250	703
38	205	403	96	1439	307	1416
40	170	220	75	409	164	295
42	72	370	107	818	253	733
44	58	244	85	413	233	1117
46	41	174	121	359	136	453
48	129	305	60	227	121	851
50	337	106	90	832	82	1093

Experiment HM2D, cages with initial frequency of 20% *D. melanogaster*

	cage A		cage B		cage C	
week	N_{mel}	N_{hyd}	N_{mel}	N_{hyd}	N_{mel}	N_{hyd}
0	20	80	20	80	20	80
2	41	247	30	192	28	144
4	14	116	68	331	29	571
6	70	558	155	398	50	648
8	183	181	205	528	78	810
10	306	992	435	546	50	1719
12	299	413	378	214	55	1067
14	—	—	—	—	—	—
16	147	411	247	479	172	817
18	138	215	171	489	243	264
20	188	144	182	54	314	264
22	321	205	121	214	520	199
24	324	469	146	295	378	171
26	186	119	303	396	271	469
28	154	294	518	406	498	389
30	170	363	449	483	305	342

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Mixed cultures (cont.)

Experiment HM2D, cages with initial frequency of 80% *D. melanogaster*

	cage A		cage B		cage C	
week	N_{mel}	N_{hyd}	N_{mel}	N_{hyd}	N_{mel}	N_{hyd}
0	80	20	80	20	80	20
2	185	22	97	36	153	23
4	128	109	74	248	246	199
6	547	129	469	493	805	278
8	460	142	337	510	463	472
10	289	538	219	704	175	1290
12	246	278	100	1026	85	605
14	—	—	—	—	—	—
16	239	487	66	569	159	1014
18	356	329	302	516	194	391
20	364	147	613	475	158	566
22	342	135	416	244	309	918
24	442	311	349	375	191	423
26	384	76	254	561	115	493
28	209	244	201	417	154	796
30	282	328	101	285	158	1030

Experiment HM1, cages with initial frequency of 20% *D. melanogaster*

	cage A		cage B		cage C	
week	N_{mel}	N_{hyd}	N_{mel}	N_{hyd}	N_{mel}	N_{hyd}
0	20	80	20	80	20	80
2	54	74	24	54	26	90
4	54	199	40	183	39	69
6	11	161	104	52	164	434
8	11	268	122	354	52	64
10	19	280	117	145	108	304
12	38	337	85	310	94	197
14	8	88	39	71	46	159
16	17	222	65	278	34	114
18	13	179	19	115	103	199
20	—	—	—	—	—	—
22	14	65	16	274	36	181
24	53	257	48	350	17	151
26	57	93	104	414	13	203
28	71	606	57	637	16	586
30	207	783	40	650	26	770
32	19	86	63	495	81	592
34	23	378	159	194	119	450
36	198	486	243	84	149	323
38	133	348	201	161	213	128
40	139	211	172	261	490	181
42	200	51	121	278	177	99
44	179	290	237	211	325	281
46	193	257	416	74	73	104
48	107	96	216	181	150	126
50	23	218	31	87	89	209

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Mixed cultures (cont.)

Experiment HM1, cages with initial frequency of 80% *D. melanogaster*

	cage A		cage B		cage C	
week	N_{mel}	N_{hyd}	N_{mel}	N_{hyd}	N_{mel}	N_{hyd}
0	80	20	80	20	80	20
2	149	45	196	27	117	51
4	173	151	193	143	147	44
6	65	155	57	105	106	116
8	43	277	68	270	126	179
10	34	130	77	90	172	88
12	52	238	59	210	228	84
14	12	148	34	63	104	122
16	7	243	60	165	41	127
18	2	148	29	69	22	67
20	—	—	—	—	—	—
22	17	128	75	129	32	144
24	*	*	63	195	60	371
26	—	—	65	601	37	209
28	—	—	59	262	170	774
30	—	—	155	263	185	138
32	—	—	254	142	172	272
34	—	—	464	83	187	226
36	—	—	249	34	303	217
38	—	—	488	170	324	144
40	—	—	687	76	428	41
42	—	—	391	29	210	130
44	—	—	372	171	500	293
46	—	—	249	137	562	39
48	—	—	151	20	147	51
50	—	—	156	173	92	124

* Cage A terminated at week 24 owing to contamination with wild-type *D. melanogaster*.

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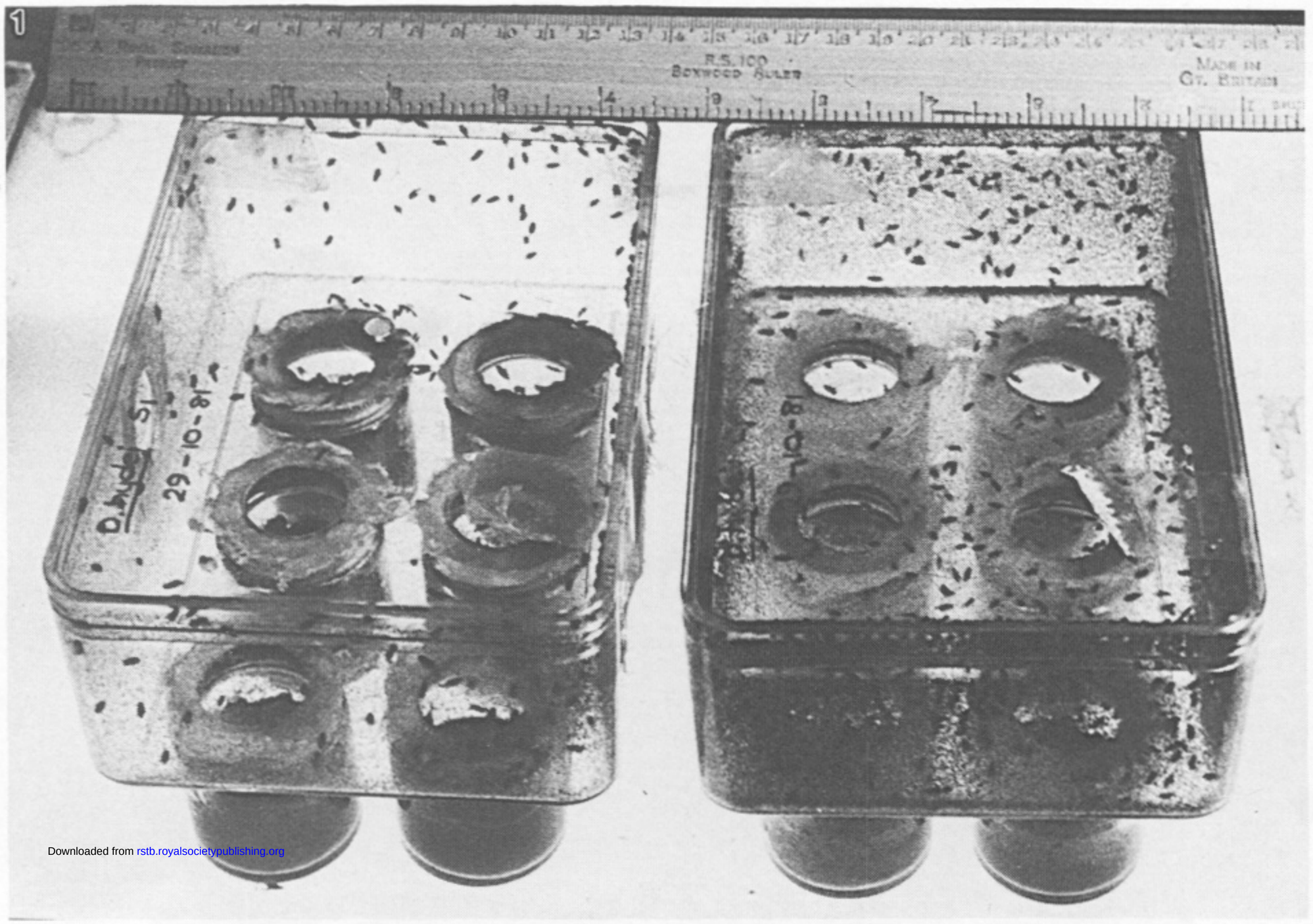

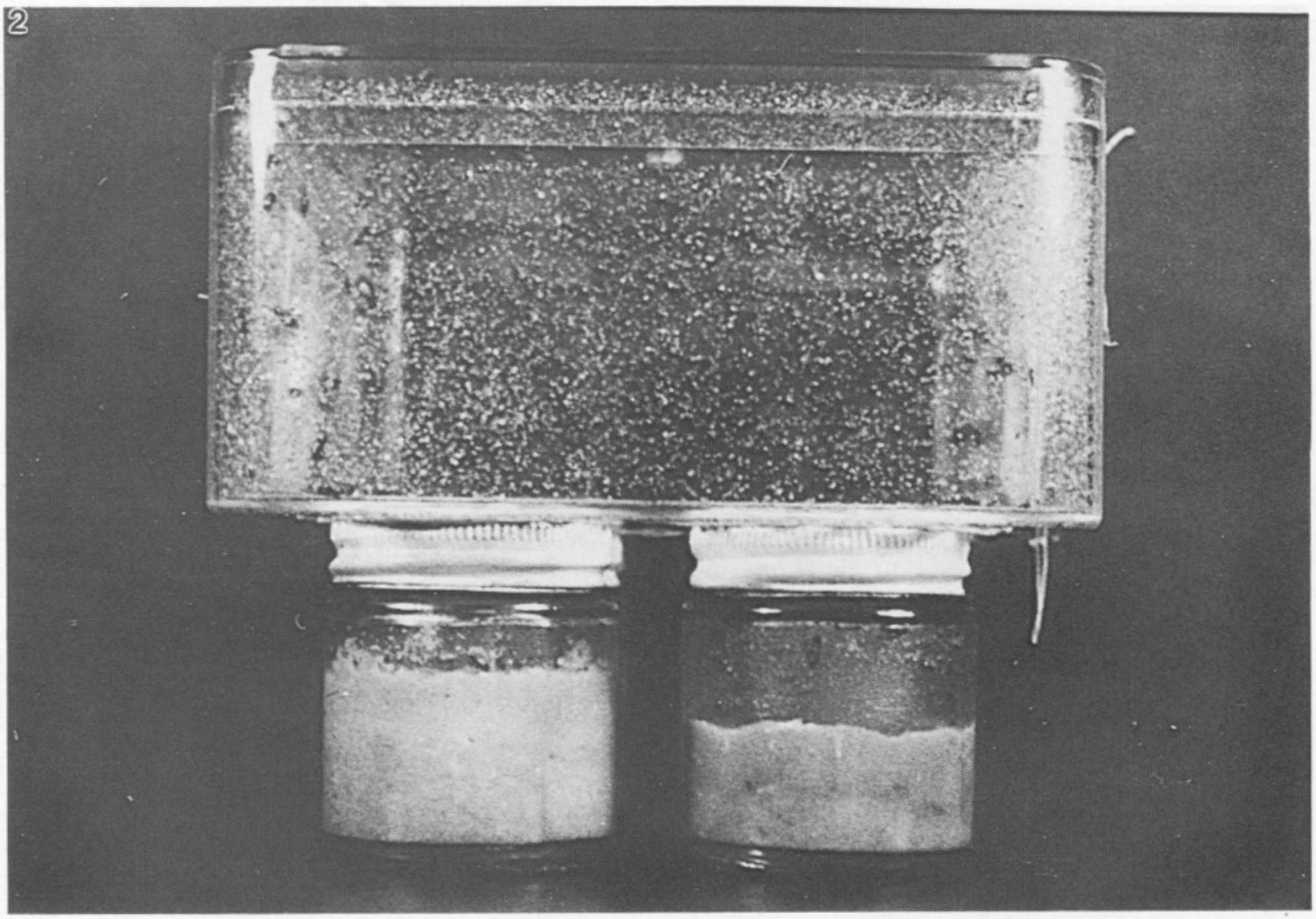

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FIGURE 1. Population cages. View from above with adults visible.

FIGURE 2. End view of population cage. Large larvae and pupae are just visible in the right-hand resource bottle.

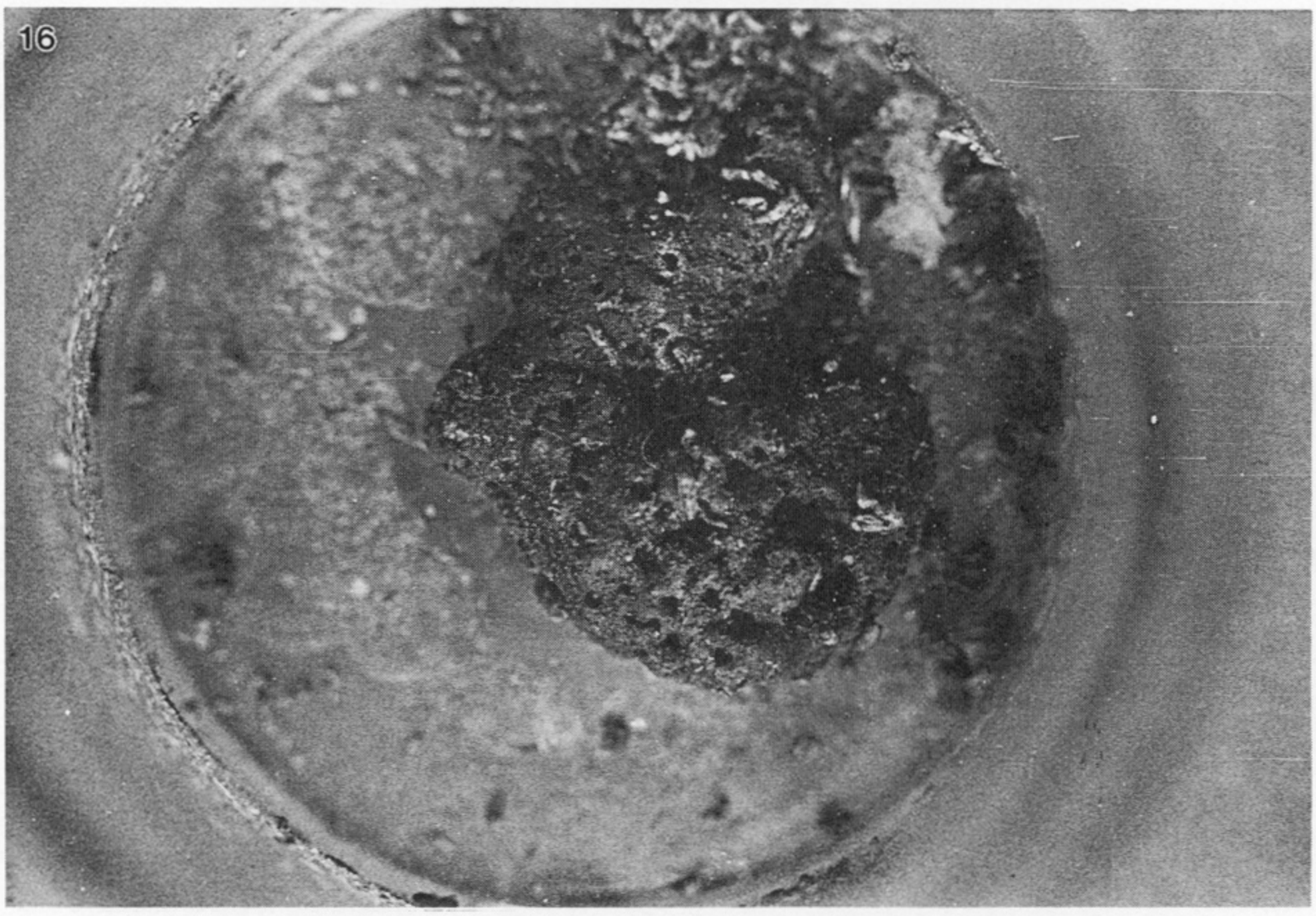

FIGURE 15. *D. hydei* monoculture in which the medium dried out before penetration of first-instar larvae.

FIGURE 16. *D. hydei* monoculture that dried out mid-way through the larval period. Note tunnels and dead, dehydrated larvae.