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Source: *Proceedings of the Royal Society of London. Series B, Biological Sciences*, Apr. 10, 1945, Vol. 132, No. 869 (Apr. 10, 1945), pp. 362-395

Published by: Royal Society

Stable URL: https://www.jstor.org/stable/82308

On competition between different species of graminivorous insects

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(*Communicated by A. D. Imms, F.R.S.—Received* 21 *March* 1944)

The growth of pure populations of the beetles *Rhizopertha dominica* and *Oryzaephilus surinamensis*, and of the moth *Sitotroga cerealella*, was observed in a standard medium of wheat. This was maintained at a constant level by the periodic removal of 'conditioned' frass and the addition of fresh grains. The population of each species rose to a maximum and remained fluctuating about this value indefinitely. A comparison of the rates of oviposition, with the rates at which adults emerged, showed that in the maximum population there was an enormous mortality (always over 90 %) in the immature stages. When pairs of species competed *Rhizopertha* eliminated *Sitotroga* because their larvae, between which most of the competition occurred, have the same needs and habits. But each of these species was able to survive with *Oryzaephilus* because this species occupies a different 'ecological niche'.

The Verhulst-Pearl 'logistic' equation (1), for the growth of population of a single species in a limited environment, and the Lotka-Volterra simultaneous equations (2), for the growth of population of two species competing for the same limited environment, were fitted to the census data from all the experiments. The biological assumptions on which they are based proved to be true for practical purposes for *Rhizopertha* and *Sitotroga* populations. These assumptions are that the value of the potential rate of increase remains statistically constant and that all the factors inhibiting increase are linearly related to population density. Furthermore, a single factor, larval competition, was represented by the single indices standing for interspecific inhibition. It follows that the maximum population (or equilibrium position) should be independent of the initial population, and this proved to be so for all species. Equations (2) did not always fit the observed points very well, but they were always successful in predicting the outcome of competition. It does not follow from this that these equations have any general validity. Their basic assumptions are by no means universally true and, unless they are shown to be so for a particular species under known environmental conditions, no biological deductions can be drawn from them. Where they do apply they describe the course of change of population of two competing organisms with an accuracy which depends on the constancy of the coefficients involved. Two kinds of organism will be able to survive together only if they differ in needs and habits, i.e. occupy different ecological niches.

Populations living in a medium of unrenewed wheat rose to a maximum and then declined as the food became exhausted and 'conditioning' increased. The eventual extinction of the population was due, not to the cessation of oviposition, but to the failure of the larvae to survive. The longevity of *Rhizopertha* adults was lower in unrenewed than in renewed medium, and lower still when this species was competing with *Sitotroga* in unrenewed medium. The longevity of the other species, and the sex ratio of *Sitotroga*, were apparently unaffected by these conditions. The fecundity of *Rhizopertha* females decreased with time, and the length of *Sitotroga* adults of both sexes decreased in succeeding generations. The competitive relationship between both *Sitotroga* and *Rhizopertha*, and *Oryzaephilus* shifted slightly in favour of the former species in unrenewed as compared with renewed media. In a renewed medium this relationship probably depends chiefly on the destruction of eggs and pupae by adults and larvae, for which the more predaceous *Oryzaephilus* is better placed. In an unrenewed medium the ability of the larvae to make the best use of the limited food supply is the determining factor, and here the other two species have the advantage. The competitive relationship between *Rhizopertha* and *Sitotroga* remained the same in both media.

1. Introduction

(*a*) *Previous investigations.* The effects of intra- and interspecific interactions (Clements & Shelford 1939) upon natality (i.e. the rate of emergence of adults from the pupa) and mortality in certain insect populations have already been described (Crombie 1942, 1943*b*, 1944). The species concerned were the beetles

Rhizopertha dominica Fab. and *Oryzaephilus surinamensis* L. and the moth *Sitotroga cerealella* Oliv. When physical conditions were constant all but one of the factors controlling population growth proved to be density-dependent (Smith 1935). The one density-independent factor was a certain mortality among *Rhizopertha* and *Sitotroga* larvae (Crombie 1944). The present paper is a study of the changes in numerical size of populations of the insects named. These changes occurred under constant physical conditions when each species was either living alone, or competing with one of the other species, for the same environment containing wheat. It may be recalled that whereas the larvae of *Rhizopertha* and *Sitotroga* have almost identical habits, both developing *inside* wheat grains, those of *Oryzaephilus* feed and develop *outside*. The adults of both beetles feed mostly outside the grains while those of *Sitotroga* do not feed. Darwin (1859, pp. 76 et seq.) pointed out that the most severe competition would occur between species which fill 'the same place in the economy of nature' or the same 'ecological niche' (Elton 1927). Competition between these species occurred chiefly among the larvae, and its main effect was to increase mortality in the immature stages (thus decreasing natality). The struggle for existence between *Rhizopertha* and *Sitotroga* may, therefore, be expected to be more severe than that between either of these species and *Oryzaephilus*.

(*b*) *A mathematical model of the competition between populations of different kinds of organism for the same environment.* The first differential of the so-called logistic equation of Verhulst and Pearl (Pearl & Reed 1920; Pearl 1925; Yule 1925) for the growth of a population of a single species in an environment of limited capacity under constant physical conditions may be written as follows:

$$\frac{dn}{dt} = bn\left(1 - \frac{n}{k}\right), \tag{1}$$

where n represents population density at any time t, k the maximum population the medium is capable of supporting, and b the potential rate of increase per unit of the population per unit time under optimum conditions [this being equal to the birth-rate (natality) minus the death-rate (mortality)]. For two species competing for the same food supply are the simultaneous equations of Volterra (1926, 1931) and Lotka (1925, 1932):

$$\frac{dn_1}{dt} = b_1 n_1\left(1 - \frac{n_1}{k_1} - \frac{\alpha n_2}{k_1}\right), \quad \frac{dn_2}{dt} = b_2 n_2\left(1 - \frac{n_2}{k_2} - \frac{\beta n_1}{k_2}\right). \tag{2}$$

Here n_1 and n_2 represent the densities of each species in the *mixed population*, b_1 and b_2, respectively, their potential rates of increase, and k_1 and k_2 the maximum population densities of each species when living *separately*. α and β are the 'competition coefficients'. While $1/k_1$ represents the proportion by which the potential increase per individual of the first species is inhibited by one individual of the same species, α_1/k_1 represents the proportion by which it is inhibited by one individual of the second species and vice versa for $1/k_2$ and β/k_2 (Gause 1934, 1935; Winsor 1934; Volterra & D'Ancona 1935; Kostitzin 1937).

A state of equilibrium between two such competing species will be reached when no further change occurs in their numbers, i.e. when $dn_1/dt = dn_2/dt = 0$. Lotka (1932) integrated equations (2) and showed that there were four possible conditions of equilibrium (Winsor 1934; Gause 1935; Kostitzin 1937):

$$(1) \quad \frac{\alpha}{k_1} < \frac{1}{k_2}, \qquad \frac{\beta}{k_2} < \frac{1}{k_1},$$

$$\lim_{t\to\infty} n_1 = \frac{k_1 - \alpha k_2}{1-\alpha\beta}, \quad \lim_{t\to\infty} n_2 = \frac{k_2 - \beta k_1}{1-\alpha\beta};$$

$$(2) \quad \frac{\alpha}{k_1} < \frac{1}{k_2}, \qquad \frac{\beta}{k_2} > \frac{1}{k_1},$$

$$\lim_{t\to\infty} n_1 = k_1, \quad \lim_{t\to\infty} n_2 = 0;$$

$$(3) \quad \frac{\alpha}{k_1} > \frac{1}{k_2}, \qquad \frac{\beta}{k_2} < \frac{1}{k_1},$$

$$\lim_{t\to\infty} n_1 = 0, \quad \lim_{t\to\infty} n_2 = k_2;$$

$$(4) \quad \frac{\alpha}{k_1} > \frac{1}{k_2}, \quad \frac{\beta}{k_2} > \frac{1}{k_1}.$$

These correspond to the following biological possibilities: (1) each species inhibits its own potential increase more than that of the other and both continue to exist together; (2) the second species inhibits the potential increase of the first less than it inhibits its own, while the first species inhibits the potential increase of the second more than it inhibits its own, whatever the initial numbers of the two species: the first species drives out the second; (3) this is the opposite to (2) and the second species drives out the first; (4) each species inhibits the other more than itself: one drives out the other depending chiefly on the initial sizes of their populations (cf. Park, Gregg & Lutherman 1941).

These four possibilities may be represented graphically by plotting the numbers of the first species along the abscissa and of the second along the ordinate (Gause 1935). The curves obtained will simply be the integral curves of equations (2). Now when $dn_1/dt = 0$, then $k_1 - n_1 - \alpha n_2 = 0$. This is the equation of a straight line on the diagram connecting all points where $dn_1/dt = 0$. This line cuts the ordinate at $n_2 = k_1/\alpha$ since here $n_1 = 0$, and the abscissa at $n_1 = k_1$ since here $n_2 = 0$. Similarly, when $dn_2/dt = 0$, $k_2 - n_2 - \beta n_1 = 0$. This line cuts the abscissa at $n_1 = k_2/\beta$ and the ordinate at $n_2 = k_2$. It is easily seen from equations (2) that at all points between the lines and the origin the values of dn_1/dt and dn_2/dt, respectively, will be positive, since here n_1 and n_2 have smaller values than those corresponding to points on the lines; while at all points on the sides of the lines remote from the origin dn_1/dt and dn_2/dt, respectively, will be negative (see figures 2 and 7).

As Gray (1929) has pointed out, a number of equations, embodying totally different theoretical assumptions, can always be fitted empirically within the limits of the experimental error to the series of observations forming a typical growth curve (cf. Bowley 1925; Teissier 1928; Winsor 1932 *a*, *b*; Bernstein 1934; Wilson 1934; Rhodes 1937, 1940; Thompson 1942, pp. 142 et seq.). Furthermore, the logistic equation can itself assume such a variety of forms that it can be made to fit almost any regularly changing series of observations (Reed & Berkson 1929; Wilson & Puffer 1933; Kavanagh & Richards 1934). It was therefore incorrect for Pearl (1924, 1925, 1927, 1937) to claim that because the logistic equation could be made to fit experimental data with considerable accuracy, it expresses the true and universal principle underlying the growth of populations of all living organisms (cf. Bodenheimer 1938). Pearl's thesis would be sustained only if it could be proved that the assumptions on which this equation is based are founded on universal biological facts (Hogben 1931). The first assumption of equation (1) is of the statistical constancy of the potential rate of increase (b) of individuals of the same nature under the same environmental conditions. This implies that when uninhibited by environmental checks, the population increases geometrically (Gray 1929; Teissier 1937). The second assumption is that all the factors which inhibit increase are density-dependent (cf. Chapman 1931, 1939; Severtzoff 1934; Smith 1935), and the third is that they are all linearly related to population density. From this it follows that an isolated population in a constant environment tends towards a finite limit which depends only upon the vital coefficients b and k, and is independent of the initial size of the population (Chapman 1928; Gause 1931). This conclusion is valid only if the circumstances affecting b and k remain unchanged (Kostitzin 1937, p. 53). In fact, none of these assumptions is true of all organisms. Populations of some organisms experience 'spontaneous' changes in reproductive vigour, viability, etc. (Clements & Shelford 1939, p. 187). In other populations reproduction is definitely periodic (Thompson 1931, 1939; Kostitzin 1937, Ch. 7). In others again the decrease in size of individuals may cause the rate of growth to assume a different value according to whether it is measured in terms of numbers or biomass (Salt 1932, 1940; Harding 1937 *a*, *b*). When the effects of the physical environment are excluded a population does not always increase until inhibited by the crowding of its own numbers (Jackson 1936). In populations where this does occur the relationships which have been observed between density and the inhibiting factors have differed quantitatively and have depended upon a number of different biological processes (cf. Pearl 1927; Teissier 1928, 1937; Allee 1934; Jahn 1934; Winsor 1937; Wilder 1940). Furthermore, the logistic equation is unable to provide any information about the age composition of a population (Winsor 1934; Lotka 1939), or to differentiate between checks to increase, between which there is no necessary connexion, which occur at different ages (Richards 1934; Kostitzin 1937; Thompson 1939). Finally, it is well known that in nature changes in environmental conditions (i.e. in the factors affecting b and k) are brought about by the organisms themselves in occupying a given medium (cf. Park 1939; Hall 1941; Medawar 1941). The logistic equation thus cannot be considered a general law of population growth

Equations (2) are based on the same assumptions as equation (1) with the addition that each species is supposed to inhibit the increase of the other in direct proportion to its own numbers. Now a single symbol (α or β) represents the factors involved in the inhibition of the increase of one species by the other. Where more than one such factor was involved only an arithmetical estimation of their combined effect would be obtained, which means that little would be learned about them individually. Equations (2) are only valid if the competitive relationship between the two species remains unaffected by changes that may occur in environmental conditions. In fact, this is not always so (Hutchinson 1941; Huxley 1942, p. 119).

In applying these equations to a particular population it is thus necessary, first, to discover whether they give an accurate empirical description of population growth, and secondly, whether the biological assumptions underlying them are true of the organisms concerned under definite experimental conditions. How this programme was carried out is described in this paper. The integrated form of equation (1) is easily fitted to population data. The simplest method of testing the fit of equations (2) is to use the differential form shown above (Gause 1934). The values of b_1, b_2, k_1 and k_2 are obtained from the logistic equations fitted to the census data for each species living alone. The values of dn_1/dt and dn_2/dt are determined from the slope of the population curves when the two species are in competition. The values of α and β may now be calculated from equations (2). Any of the parameters so calculated (preferably over as great a range as possible) may be compared with the values obtained independently from direct observation of the particular factors which the parameters are supposed to represent. The degree of accuracy to which the equations both fit the observations and describe real biological processes is thus established.

2. TECHNIQUE

These experiments were all performed in a dark incubator at 30° C and 70 % R.H. Other technical precautions were similar to those described in a previous paper (Crombie 1942).

The changes in adult population size which occurred when a species was either living alone, or competing for the same environment with another species, were studied as follows. All populations lived in standard environments of 10 g. (200 grains) of wheat in jars of standard size (6·5 cm. diam. × 5·5 cm. high). The mouth of each jar was covered with a piece of muslin held on with a rubber ring. The wheat was cracked in order to make conditions here similar to those in previous experiments on larval competition (Crombie 1944). This condition holds in all the experiments described below unless otherwise stated. Parallel populations of *Rhizopertha* and *Sitotroga* were observed in intact wheat in order to see whether the cracking of the wheat introduced any important difference into the conditions. The results, however, were essentially similar with both types of grain (vide infra). The wheat medium was renewed in some experiments but not in others. When it was renewed the food supply was limited but constant; when unrenewed the food supply decreased and the medium became more 'conditioned' with time. Experimental populations were set up with each species alone and in competition. In the latter the initial numbers of each species were varied in different experiments. There were two or more identical jars for each experiment. Each census value given in the tables is the mean of the counts in those parallel jars.

The sex ratio of the original *Rhizopertha* and *Oryzaephilus* adults was always unity and except when the initial number of adults was 50 or over the females of each species were of standard fecundity 6–8 and 3–4 eggs per female per day, respectively. In some experiments (see tables) *Rhizopertha* eggs (of various ages) were added originally. Then fifty eggs added once a week for 5 weeks (= 250 eggs in all) were considered equivalent to one female ovipositing at the rate of seven eggs per day. Because of the great variability in fecundity of individual *Sitotroga* females, eggs (of various ages) of this species were always added originally, 100 eggs being considered equivalent to one female (cf. Crombie 1942).

The jars containing the experimental populations were examined at regular intervals of 7 days. At each examination the wheat was gently shaken in a sieve of no. 52 (extra quadruple) silk bolting cloth, which allowed the frass material to pass through while retaining the eggs and larvae of both species. When the medium was renewed the material passing through the sieve was discarded. The material retained consisted of wheat and insects. The food supply was renewed every 7 days, but population counts were usually made every 14 days. On the days when counts were not made the material retained by the sieve was placed on a balance and brought up to the original 10 g. by the addition of fresh cracked wheat. This was then replaced in the jars, and the jars in the incubator. On the days when counts were made the living and dead adult insects were removed and counted, the wheat (which contained larvae and pupae) placed on a balance and fresh cracked wheat added to bring its weight up to 10 g. again. The wheat and the living adults were then replaced in the jar and all returned to the incubator. Thus records were obtained of the total number of living adults in the population after regular intervals of time from the beginning of the experiment, and of the number dying between each count. The nature of the medium prevented the counting of immature stages. A record was also kept of the amount of fresh food added at each examination. By this method the food supply was maintained at a constant level, and conditioning of the medium reduced, but not entirely eliminated. When the medium was unrenewed a slightly different technique was used (vide infra).

3. THE COMPETITION OF *RHIZOPERTHA* AND *SITOTROGA* IN RENEWED MEDIA

(*a*) *The growth of populations of* Rhizopertha *and* Sitotroga *living separately* (*medium renewed*). The original insects were introduced into their respective jars on the first day of the experiment. There were four jars containing each species.

The initial number of *Rhizopertha* was two adults and of *Sitotroga* 100 eggs. The growth of populations of these species is shown in table 1 *a*, *b* and figure 1. The *Rhizopertha* values represent adults found alive at each count. The somewhat violent fluctuations in the numbers of *Sitotroga* are due to the short duration of the adult instar in these insects, so that many of the adults of one generation died before those of the next generation emerged. For this reason the total number of adults (living and dead) found at each count is given in the table. This gives a measure of the size of each generation, the peaks representing successive generations. The distance between adjacent peaks is 30–40 days, which is in agreement with previous determinations of the generation time of *Sitotroga* with the same conditions of food, temperature, and humidity (Crombie 1943*a*). The adult population of *Rhizopertha* and the generation maxima of *Sitotroga* adults each increased until maxima were reached, then remained constant.

From the number of dead individuals found at each count it is easy to calculate the average longevity from the adults if it be assumed that the oldest die first. The average longevity of *Rhizopertha* adults proved to be 159 days. Individuals apparently varied considerably, extremes being 65 and 203 days. No reduction of longevity at the higher densities was apparent. This is possibly because the time taken for the population to reach its maximum is about equal to the average longevity of the adults, so that even adults of the first generation would be exposed to practically the maximum density for a large proportion of their lives. The average longevity of this species was also unaffected by competition with *Sitotroga*. The calculation of *Sitotroga* longevity by this method is rendered very unreliable by the infrequency of the counts as compared with the length of adult life of this species, but the results obtained show that the average value was approximately the same as that previously observed, viz. 6·6 days (Crombie 1942, 1943*a*). From the same data it is also possible to calculate the average rate of adult mortality per adult per day in the maximum population. In *Rhizopertha* this proved to be approximately 0·0046. This mortality rate varied from time to time, extremes being 0·00068–0·007. In a population which is not changing in size adult mortality is equal to natality, so that in the maximum population natality (rate of emergence of adults) would also be equal to 0·0046 per adult per day. Now in this population there were 1·7 adults per grain, and at this density the average fecundity is approximately three eggs per adult per day (Crombie 1942). A very high mortality, amounting approximately to 2·9954 individuals per female per day or 99·85% of the eggs oviposited, must therefore occur in the immature stages after the population has reached the maximum (cf. Graham 1939). There is considerable overlapping of generations in the *Rhizopertha* populations, so that mortality and natality may be regarded as practically continuous in time. Reproduction and death in *Sitotroga*, however, are definitely periodic and clearly marked off into separate generations. Nevertheless, similar information may be obtained about this species from the numbers of individuals in each generation. In one particular population the first filial generation consisted of sixty-two individuals, of which thirty were females. If it be assumed that each female lays 100 eggs in its life then that generation will produce 3000 eggs which will go to form the second generation. The second generation which emerged consisted, however, of only 286 adults, showing that there was a mortality in the immature stages of 2714 individuals, or 90·5 % of the eggs oviposited. In *Sitotroga*, whose adults do not feed, this mortality would be caused chiefly by larval competition which is density-dependent, but about 7 % of the larval mortality is due to causes which are density-independent (Crombie 1944). In *Rhizopertha* both larval competition and adult feeding may cause larval mortality (cf. MacLagan & Dunn 1935). Now 200 wheat grains support maximum of 338 *Rhizopertha* and 200 *Sitotroga*, respectively. The amount of medium which supports one *Sitotroga* throughout development therefore supports 338/200 = 1·69 *Rhizopertha* throughout development and as adults. During larval development *Rhizopertha* consumes 11·5 mg. and *Sitotroga* 18·6 mg. of wheat per individual (Crombie 1944). The amount of wheat which supports one *Sitotroga* larva thus supports 18·5/11·5 = 1·61 *Rhizopertha* larvae. This is extremely close to 1·69. Now it seems that most of the larvae which do not survive competition (to be counted as adults in table 1) die in an early stage before they can make very much impression on the food supply (Crombie 1944). It follows therefore that since the adults of the two species appear (in table 1 *a*, *b*) in the proportion at which their larvae consume food, the *Rhizopertha* adults must feed chiefly upon grains which are already useless for larval development. This is possible since the larvae of both species require certain mechanical conditions for development which would be destroyed before the food value of the grains had been exhausted. The feeding of *Rhizopertha* adults would thus appear to be a relatively unimportant factor in interspecific competition.

(*b*) Rhizopertha *and* Sitotroga *in competition* (*medium renewed*). Two *Rhizopertha* adults and 100 *Sitotroga* eggs were introduced together into two jars containing cracked wheat. The subsequent growth of the population is shown in table 1*c*. At first, when density was low, the rate of growth of *Rhizopertha* was reduced while that of *Sitotroga* was as great as that when it was living alone. Eventually, however, the *Sitotroga* were driven out, while the *Rhizopertha* went on increasing and reached a maximum of the same value as when this species was living alone. The *Rhizopertha* then entirely occupied the medium and continued to exist alone. Now larvae of *Rhizopertha* have an advantage over larvae of *Sitotroga* with which they are in competition (Crombie 1944). Each generation will therefore see a larger proportion of *Rhizopertha* among the survivors (cf. Crombie 1943*b*). Furthermore, the adults of *Rhizopertha* are long lived and have an oviposition period of several months, whereas *Sitotroga* live for only a few days. Thus the outcome of competition between any particular generation of larvae is accumulative for *Rhizopertha*, while in *Sitotroga* it affects only the immediately succeeding generation. The result is that as time passes the *Rhizopertha* adults, and consequently their larvae, become increasingly more numerous than those of *Sitotroga*. This reduces the chance of survival of larvae of the latter species (Crombie 1944).

TABLE 1. THE GROWTH OF POPULATIONS OF *RHIZOPERTHA* AND *SITOTROGA* IN WHEAT. MEDIUM RENEWED

	(*a*) *Rhiz.*	(*b*) *Sit.*	(*c*) 2 *Rhiz.* v. 2 *Sit.*		(*d*) 2 *Rhiz.* v. 2 *Sit.* (intact wheat)	
days	alone	alone	*Rhiz.*	*Sit.*	*Rhiz.*	*Sit.*
0	2	100 eggs*	2	100 eggs	250 eggs	100 eggs
14	2	0	2	0	0	0
28	2	5	2	12	0	5
35	3	15	3	38	2	12
42	17	51	13	54	19	19
49	65	59	37	12 (70)	22	3
56	—	15	—	—	—	—
63	119	58	58	44 (92)	22	26
77	130	185	72	109	26	110
84	—	114	—	(74)	—	—
91	175	68	98	38	42	30
105	205	151	141	39	75	56
119	261	200	205	36	134	70
133	302	130	238	15	152	34
147	330	206	288	9 (15)	195	31
161	315	178	290	15	220	15
175	333	110	320	7	260	21
189	350	180	320	8	279	11
203	332	120	260	3	315	9
231	333	200	320	6	327	3
345	335	—	310	4	342	7
259	330	—	340	2	330	4
273	—	—	300	0	324	2
287	—	—	300	0	332	0

* In tables 1, 2, 3, 5, 7 and 8 the figures refer to adults except where eggs are specially mentioned.

The feeding of *Rhizopertha* adults is apparently not an important factor in interspecific competition, but the possibility remains that it may have some effect. The average rate of feeding of *Rhizopertha* adults is 1·7 mg. per adult per day (Crombie 1942). This does not represent the rate at which food is ingested, since much of the material is merely chewed off the grains while the adults are burrowing into them, but it does represent the rate at which grains as such are destroyed. The average weight of a wheat grain is 50 mg., so that the average time taken for one adult to destroy one grain is 29·5 days. It would, however, be rendered useless for larval development before its complete destruction. *Rhizopertha* adults will also kill *Sitotroga* pupae if they happen to be present. The average period from hatching to emergence for *Sitotroga* is 29 days (Crombie 1943*a*). Since the medium contains 200 wheat grains (10 g.), by the time the *Rhizopertha* adult population was approximately 200 all the fresh grains may have been destroyed 29·5 days after they were added to the medium. After the *Rhizopertha* population has reached this value the *Sitotroga* would therefore be completely inhibited if the

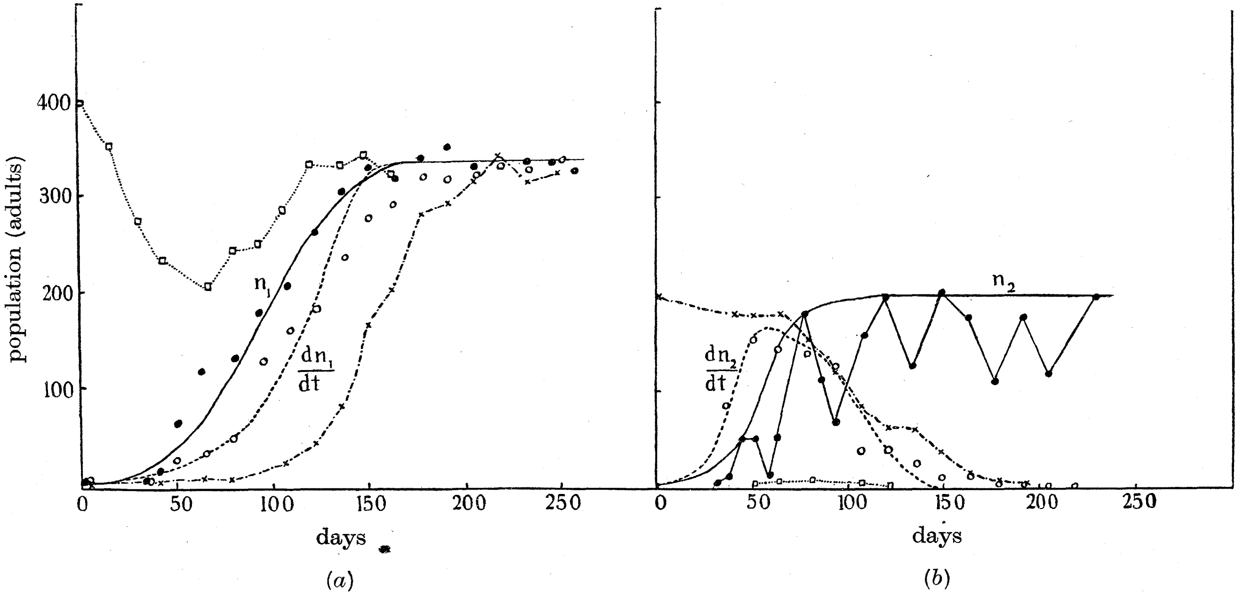

Figure 1. The growth of populations of (*a*) *Rhizopertha* (n_1) and (*b*) *Sitotroga* (n_2) in wheat (medium renewed). ●, separately (table 1*a*, *b*); ○, 2 *Rhizopertha* versus 20 *Sitotroga* (table 3*a*); □, 400 *Rhizopertha* versus 2 *Sitotroga* (table 2*h*); ×, 2 *Rhizopertha* versus 200 *Sitotroga* (table 3*e*). Three of the *Sitotroga* points have been smoothed as shown in table 3*a*, *e*.

$$n_1 = 338/(1+87e^{-0\cdot05t}), \quad dn_1/dt = 0\cdot05n_1(338-n_1-n_2)/338;$$
$$n_2 = 200/(1+257e^{-0\cdot1t}), \quad dn_2/dt = 0\cdot1n_2(200-n_2-1\cdot3n_1)/200.$$

Rhizopertha adults did not feed mostly upon grains already useless for larval development. *Rhizopertha* has thus three advantages over *Sitotroga,* but the superiority of its larvae in competition is seemingly much the most important.

This experiment was now repeated using intact wheat. The adults of *Rhizopertha* are unable to attack these grains, so that the initial *Rhizopertha* were introduced by adding eggs (vide supra). At the end of 5 weeks the first generation of adults was beginning to emerge. The outcome of competition was essentially the same as in cracked wheat, but the suppression of the *Sitotroga* took longer and the initial increase of the *Rhizopertha* was slower (table 1*d*). Now the first instar larvae of both species are able to enter the intact grains. The final expulsion of *Sitotroga* could not have been due to the feeding of the *Rhizopertha* adults, since they would not have been able to attack the fresh intact grains added at regular intervals, although they may have destroyed grains which had already been damaged by larvae. The expulsion of the *Sitotroga* from the latter grains may thus possibly have been due to the feeding of the *Rhizopertha* adults, but their expulsion from the fresh intact grains must be attributed to the competition of *Rhizopertha* larvae.

The foregoing experiments show that when equal numbers of *Rhizopertha* and *Sitotroga* adults invade a medium of wheat grains at the same time, the *Sitotroga* are eventually driven out and the *Rhizopertha* continue to exist alone. In the next experiments the initial numbers of each species were unequal, the initial population of the more numerous species having various values up to approximately the value of the maximum population of that species when it was living alone.

First, while the initial number of *Sitotroga* introduced remained constant at 100 eggs (= 1 fertilized female), the initial number of *Rhizopertha* varied from 10 to 400 adults (or an equivalent number of eggs) as shown in table 2 and figure 1. Two parallel jars were set up for each experiment. In every experiment the *Sitotroga* were eventually driven out while the *Rhizopertha* population rose to a maximum of approximately 338 and continued to exist alone. The *Rhizopertha* population increased at a slower rate and the *Sitotroga* survived longer in intact than in cracked wheat. In table 2*h* the *Rhizopertha* population, which was initially above maximum density, declined before rising again to the maximum of approximately 33·8 adults per gram. When the medium was renewed the limiting population was thus independent of the initial population, which as we have seen is a characteristic of populations which grow according to the 'logistic rule' (Chapman 1928; Gause 1931). Even when the initial *Rhizopertha* population saturated the medium a few *Sitotroga* survived. This would be expected from the hyperbola-like relationship which was found to exist between the initial density of *Rhizopertha* larvae and the proportion of *Sitotroga* larvae surviving (Crombie 1944).

In the next experiments the initial *Rhizopertha* consisted of either two adults or 250 eggs, added as before (vide supra). The initial number of *Sitotroga* was increased from 1000 eggs (= 20 adults) to 10,000 eggs (= 200 adults) as shown in table 3 and figure 1. The *Sitotroga* eggs were added in equal numbers every day for

TABLE 2. THE GROWTH OF POPULATIONS OF *RHIZOPERTHA* AND *SITOTROGA* IN WHEAT. *RHIZOPERTHA* INITIALLY MORE NUMEROUS. MEDIUM RENEWED

	(*a*) 10 *Rhiz.* v. 2 *Sit.*		(*b*) 20 *Rhiz.* v. 2 *Sit.*		(*c*) 20 *Rhiz.* v. 2 *Sit.*		(*d*) 20 *Rhiz.* v. 2 *Sit.* (intact wheat)	
days	*Rhiz.*	*Sit.*	*Rhiz.*	*Sit.*	*Rhiz.*	*Sit.*	*Rhiz.*	*Sit.*
0	10	100 eggs	20	100 eggs	2500 eggs	100 eggs	2500 eggs	100 eggs
14	10	0	0	0	0	0	0	0
28	10	21	20	10	5	11	4	17
42	55	60	54	50	52	46	40	32
49	64	58	77	60	122	49	62	30
63	99	31 (55)	135	30 (56)	146	15 (48)	75	15
77	156	53	168	60	205	49	160	35
84	—	—	—	—	—	—	—	—
91	195	45	183	41	235	33	173	22
105	220	19	195	20	260	13	210	18
119	260	6 (14)	236	21	311	4	252	10
133	310	10	274	8 (16)	338	0	276	5
147	328	4	295	12	330	2	300	13
161	337	5	337	2	347	0	320	6
175	328	2	334	2	340	0	337	2
189	342	0	328	0	—	—	342	0
203	336	0	342	0	—	—	314	2
217	—	—	—	—	—	—	336	0

	(*e*) 50 *Rhiz.* v. 2 *Sit.*		(*f*) 50 *Rhiz.* v. 2 *Sit.* (intact wheat)		(*g*) 50 *Rhiz.* v. 2 Sit.		(*h*) 400 *Rhiz.* v. 2 *Sit.*	
days	*Rhiz.*	*Sit.*	*Rhiz.*	*Sit.*	*Rhiz.*	*Sit.*	*Rhiz.*	*Sit.*
0	6500 eggs	100 eggs	6500 eggs	100 eggs	250	100 eggs	400	100 eggs
14	0	0	0	0	250	0	350	0
28	0	0	0	0	250	3	275	5
42	15	5	4	5	190	16	—	—
49	46	2	18	4	—	—	235	5
63	111	1	54	6	190	9 (16)	205	6
77	176	17	116	19	210	16	245	5
84	205	24	165	25	—	—	—	—
91	225	17	—	—	235	16	250	2
105	235	12	170	16	220	9	286	1
119	278	9	205	14	240	10	332	0
133	268	7	245	8	270	7	330	0
147	290	2	255	3	300	2	341	0
161	305	2	260	8	334	0	322	0
175	309	2	310	9	322	0	—	—
189	336	1	342	2	330	0	—	—
203	330	0	334	3	320	0	—	—
217	325	0	334	0	—	—	—	—

3 days. Two parallel jars were set up for each experiment. The *Rhizopertha* always drove out the *Sitotroga* in cracked wheat. The outcome of competition in intact wheat (table 3*d*) was essentially similar to that in cracked wheat in the jars in which *Rhizopertha* adults appeared at all. The growth of the *Rhizopertha* was somewhat slower and the period of survival of *Sitotroga* somewhat longer in the former than in the latter. But in one of the two parallel jars containing intact wheat no *Rhizopertha* adults appeared at all. The experiment was therefore repeated with eight more similar jars containing intact wheat. In two out of these eight jars no *Rhizopertha* appeared, while in the other six the results were the same as in the other jar in which this species survived. The values in table 3*d* are the averages of the seven jars in which *Rhizopertha* survived. In the other three (out of ten) the *Rhizopertha* larvae were evidently overwhelmed by the superior numbers of *Sitotroga* larvae, possibly because many of them died in attempting to enter the grains. Many of the wheat grains in which *Sitotroga* had lived for one generation would have been damaged by the emergence of the adults. In nature the *Rhizopertha* larvae would therefore never find themselves competing with overwhelming numbers of *Sitotroga* for a medium consisting entirely of intact grains. In table 3*d*, from the 42nd to the 84th day, never more than two *Rhizopertha* adults were in competition in intact wheat with populations of *Sitotroga* almost equal to the maximum reached in table 1*b*, yet the *Sitotroga* were eventually driven out. It may be concluded therefore that even in a medium of intact wheat, if one adult *Rhizopertha* survives and is fertilized by a surviving male, the *Sitotroga* will eventually be driven out. In table 3*e* there were initially 10,000 *Sitotroga* eggs (= 200 adults) and 250 *Rhizopertha* eggs. Here some of the *Rhizopertha* survived in both jars, eventually drove out the *Sitotroga*, and rose to a maximum population of approximately 338 adults. Now 200 adults is the maximum population for *Sitotroga* living alone, so that the maximum number of eggs oviposited in one generation by a population of *Sitotroga* is not likely to exceed 10,000. But even when *Sitotroga* had this numerical superiority some of the *Rhizopertha* larvae survived to become adults. It may be argued that the survival of the *Rhizopertha* larvae even at that initial numerical disadvantage was due to the fact that whereas the 10,000 *Sitotroga* eggs were all introduced in the first 3 days, the *Rhizopertha* eggs were introduced over a period of 5 weeks. The *Rhizopertha* introduced after the third week would then encounter only the late larval instars or the pupae of the *Sitotroga*, and competition against them would be less severe (Crombie 1944). However, from the 28th to the 77th day the population of *Sitotroga* adults was maintained at between 80 and 185, while there were only one to three *Rhizopertha* adults over this period. The larvae produced by these few *Rhizopertha* adults had therefore to compete with *Sitotroga* larvae of all ages, with much the same numerical disadvantages as initially. It may therefore be concluded that if one male and one female *Rhizopertha* survive from the larvae introduced into a maximum population of *Sitotroga*, which is the greatest numerical disadvantage the *Rhizopertha* would have to endure, the *Sitotroga* will eventually be driven out, and the *Rhizopertha*

population will rise to an asymptotic value and continue alone (cf. D'Aeth 1939). Finally, in table 3*f* there were initially 50 adult *Rhizopertha* and 2500 *Sitotroga* eggs. The *Sitotroga* were eventually driven out as before.

The competition of *Sitotroga* reduces the rate of growth of the *Rhizopertha* population roughly in proportion to the initial numbers of the former. This may be seen from an examination of the time taken by the latter to pass the turning point in the growth curve, which occurs at a population of approximately 169 adults. Thus in cracked wheat when there were initially numbers of *Sitotroga* eggs equivalent to 0, 2, 20, 50 and 200 adults, the times taken by the *Rhizopertha* population (initially two adults) to pass this value were 91, 119, 119, 119, and 161 days, respectively. In intact wheat with initially two *Rhizopertha* adults and eggs equivalent to two and fifty *Sitotroga* adults, the times taken by the *Rhizopertha* population to increase above 169 were 147 and 189 days, respectively. In cracked wheat with initially 50 *Rhizopertha* adults and eggs equivalent to two and fifty *Sitotroga* adults, the length of this period was 77 and 105 days, respectively. The longevity of the *Rhizopertha* adults was not affected by competition with *Sitotroga*.

(*c*) *Mathematical model of* Rhizopertha *and* Sitotroga *populations*. Let *Rhizopertha* be the first species (n_1) and *Sitotroga* the second species (n_2). Logistic curves were fitted to the census data for each species shown in table 1 *a* and *b*, respectively. The equations obtained are given in figures 1 *a* and *b*, respectively. The asymptotic population (k_1) for *Rhizopertha* was 338 and the potential rate of increase (b_1) 0·05. The *Sitotroga* population showed distinct generations, and such a population does not increase geometrically (Thompson 1931, 1939; Richards 1934; Winsor 1934; Kostitzin 1937). It is conceivable, however, that the generation maxima may increase geometrically and the logistic curve was consequently fitted to these. This procedure greatly reduced the number of points and consequently the accuracy of the curve which was fitted to them. The asymptotic population (k_2) here was 200 and the potential rate of increase (b_2) 0·1. The values of all the terms in equations (2) are now known except α, β, dn_1/dt and dn_2/dt. The values of the two latter terms may be determined by measuring the tangents to the curves of population growth, but sufficiently accurate values were obtained as follows: three censuses equidistant in time were selected. The value of dn/dt at the middle point was then given by the difference in the size of the population (n) between the two extreme points divided by the period of time between them. Before calculating the slope in this way the points on the *Sitotroga* curve between generation maxima were smoothed, the interpolated points appearing in brackets in the tables. From these values of dn_1/dt and dn_2/dt the values of α and β were then calculated from equations (2). Such calculations were made at all points in the middle region of population growth from the data in Tables 1–3. The indices α and β are, however, particularly sensitive to small fluctuations in population size, and the values of b_1 and b_2 were therefore also calculated at the same points with fixed values of $\alpha = 1$ and $\beta = 1{\cdot}3$. The latter are the average values obtained from table 1*c*, and are also equal to the average values for all the tables mentioned in table 4 except

TABLE 3. THE GROWTH OF POPULATIONS OF *RHIZOPERTHA* AND *SITOTROGA* IN WHEAT. *SITOTROGA* INITIALLY MORE NUMEROUS. MEDIUM RENEWED

	(*a*) 2 *Rhiz.* v. 20 *Sit.*		(*b*) 2 *Rhiz.* v. 50 *Sit.*		(*c*) 2 *Rhiz.* v. 50 *Sit.*	
days	*Rhiz.*	*Sit.*	*Rhiz.*	*Sit.*	*Rhiz.*	*Sit.*
0	2	1000 eggs	2	2500 eggs	250 eggs	2500 eggs
14	2	0	2	0	0	0
28	1	7	0	20	0	15
35	4	90	2	95	0	38
42	—	—	—	—	0	80
49	28	155	13	180	2	136
63	37	80 (148)	22	73 (190)	3	96
77	46	95 (140)	32	72 (200)	3	140
91	130	130	78	213	4	110
105	160	44	140	74	27	118
119	185	47	172	55	51	85
133	240	29	212	41	89	56
147	282	11	244	26	191	50
161	292	12	272	17	238	30
175	322	5	296	8	289	14
189	321	2	320	4	318	8
203	327	0	330	0	330	3
217	331	1	322	2	339	1
231	326	0	337	0	328	0
249	337	0	321	0	334	0
263	—	—	—	—	—	—
277	—	—	—	—	—	—
291	—	—	—	—	—	—
305	—	—	—	—	—	—
319	—	—	—	—	—	—
333	—	—	—	—	—	—

	(*d*) 2 *Rhiz.* v. 50 *Sit.* (intact wheat)		(*e*) 2 *Rhiz.* v. 200 *Sit.*		(*f*) 50 *Rhiz.* v. 50 *Sit.*	
days	*Rhiz.*	*Sit.*	*Rhiz.*	*Sit.*	*Rhiz.*	*Sit.*
0	250 eggs	2500 eggs	250 eggs	10000 eggs	50	2500 eggs
14	0	0	0	0	50	0
28	0	11	0	100	40	40
35	0	20	—	—	31	105
42	0	115	1	185	—	—
49	0	170	1	80 (185)	48	95
63	1	85	3	184	95	37 (98)
77	2	120	3	156	141	100
91	2	170	4	120	160	15 (59)
105	13	110	26	86	200	18
119	23	104	42	64	258	11
133	30	130	78	62	312	0
147	82	120	163	38	328	0
161	115	42	209	18	339	2
175	155	32	276	7	332	0
189	199	52	292	5	326	0
203	260	19	326	4	—	—
217	307	15	342	0	—	—
231	336	8	315	4	—	—
249	329	6	327	0	—	—
263	315	2	—	—	—	—
277	324	4	—	—	—	—
291	324	4	—	—	—	—
305	332	2	—	—	—	—
319	346	0	—	—	—	—
333	338	0	—	—	—	—

table 3 *c* and *e* (vide infra). The average values of α, β, b_1 and b_2 calculated during the periods indicated are given in table 4. The small values of n_1 or n_2 at the beginning and end of population growth sometimes lead to violent random fluctuations in value of one or more of these indices. Values obtained in these regions which were widely different from the rest were consequently omitted when calculating the averages. All the values obtained from table 2 *g* and *h* are also omitted for the same reason. Individual values of all four indices fluctuate a good deal, but this is to be expected since they are calculated from the census points, not from smoothed curves. The ranges of fluctuation are given in brackets in table 4. There is no regular change in value of b_1, b_2 or α with time. The value of β is sometimes rather large at the beginning of population growth, then gradually decreases to normal values. The probable reason for this is that at first the *Sitotroga* were inhibited by *Rhizopertha* larvae which had not yet emerged as adults and been counted. The population of *Rhizopertha* used in calculating β early in population growth is thus much smaller than the one which is actually competing against *Sitotroga*. In table 3 *c* and *e* this effect is so great that all the indices are affected: b_1 and β become too large, b_2 and α too small. The values of b_2 and β return to normal as the *Rhizopertha* adult population increases, but b_1 and α remain abnormal because the increase in the latter population is rapid from a low value. The census of adults alone is thus sometimes defective as a measure of the behaviour of the whole population.

The data which equations (2) fit most accurately when $b_1 = 0{\cdot}05$, $b_2 = 0{\cdot}1$, $\alpha = 1$ and $\beta = 1{\cdot}3$ are those in table 3*a*. The curves fitted to these data are shown in figure 1. These coefficients do not remain sufficiently constant for the equations to fit the data in the other tables equally well (see figure 2). Now $k_1/k_2 = 338/200 = 1{\cdot}69$ and $k_2/k_1 = 200/338 = 0{\cdot}59$. The average values of α and β shown in table 4 all satisfy the inequalities $\alpha < k_1/k_2$ and $\beta > k_2/k_1$ (or $\alpha/k_1 < 1/k_2$ and $\beta/k_2 > 1/k_1$). These inequalities correspond to the second condition of equilibrium for equations (2) (vide supra), in which $n_1 \to k_1$ and $n_2 \to 0$, whatever the initial values of n_1 and n_2. This is what actually happened in these experiments. In figure 2 n_1 is plotted against n_2 (smoothed points). The straight lines connecting points where dn_1/dt and dn_2/dt, respectively, are zero intersect the ordinate and abscissa at the following points, respectively: $n_2 = k_1/\alpha = 338$, $n_1 = k_1 = 338$; and $n_2 = k_2 = 200$, $n_1 = k_2/\beta = 154$. The turning points of the observed curves usually fall near the line representing $dn_2/dt = 0$, and the curves rarely escape from the region between the two straight lines. Equations (2) may thus be used to predict the outcome of competition, although the theoretical curves are not always accurately followed by the populations.

Now the fecundity of *Sitotroga* is not reduced at densities possible in actual populations, while in unconditioned media the reduction in the fecundity of *Rhizopertha* which occurs between 0·25 and 1·5 insects per grain (i.e. from the 50th day of population growth in table 1*a*) is unimportant compared to the larval mortality (Crombie 1942). It is easy to calculate from the known fecundities of these species

Table 4. Average values of α, β, b_1 and b_2 during the competition of *Rhizopertha* (n_1) and *Sitotroga* (n_2)

table	range of days	α ($b_1 = 0{\cdot}05$)	β ($b_2 = 0{\cdot}1$)
1*c*	35–175	1·05 (0·36–1·84)	1·28 (0·64–3·00)
2*a*	42–133	0·82 (0·11–1·58)	1·17 (0·84–1·75)
2*b*	42–147	0·74 (– 1·1–3·35)	1·11 (0·75–1·8)
2*c*	42–105	0·92 (0·54–1·4)	1·14 (0·42–2·0)
2*e*	84–105	1·08	0·93 (0·86–1·0)
3*a*	49–161	1·05 (– 0·03–2·16)	1·46 (0·67–3·35)
3*b*	49–161	1·03 (0·49–1·34)	1·08 (0·37–2·0)
3*c*	105–175	– 0·9 (– 2·34–0·03)	2·05 (0·98–3·6)
3*c*	147–175	– 0·9 (– 1·29–0·03)	1·03 (0·98–1·07)
3*e*	105–161	– 0·02 (– 0·5–1)	3·04 (1·45–6·2)
3*e*	147–161	0·25 (– 0·5–1)	1·5 (1·45–1·5)
3*f*	49–119	1·65 (– 0·33–1·5)	1·27 (0·26–2·3)

table	range of days	b_1 ($\alpha = 1$)	b_2 ($\beta = 1{\cdot}3$)
1*c*	35–175	0·055 (0·039–0·089)	0·076 (0·05–0·1)
2*a*	42–133	0·07 (0·023–0·113)	0·055 (0·03–0·096)
2*b*	42–147	0·049 (0·010–0·083)	0·051 (0·011–0·098)
2*c*	42–105	0·057 (0·04–0·081)	0·061 (0·016–0·11)
2*e*	84–105	0·042 (0·029–0·054)	0·058
3*a*	49–161	0·053 (0·03–0·091)	0·107 (0·026–0·186)
3*b*	49–161	0·061 (0·044–0·089)	0·088 (0·037–0·126)
3*c*	105–175	0·09 (0·071–0·098)	– 0·024 (– 0·16–0·061)
3*c*	147–175	0·088 (0·071–0·097)	0·066 (0·037–0·061)
3*e*	105–161	0·073 (0·059–0·094)	0·026 (– 0·086–0·166)
3*e*	147–161	0·065 (0·059–0·011)	0·153 (0·139–0·166)
3*f*	49–119	0·064 (0·038–0·082)	0·154 (– 0·017–0·59)

that larval density would have exceeded eight larvae per grain before the 50th day of population growth. For both species the relationship between larval mortality and density during both intra- and interspecific competition is practically linear at densities above this value (Crombie 1944, Fig. 3). Therefore during almost the whole of population growth larval mortality is linearly related to larval, and if fecundity be considered to remain constant, to adult population density. At the beginning of population growth the inhibiting factors are not linearly related to density. In this region too there is the possibility that the *Rhizopertha* generations are more distinct. These conditions may be partly responsible for the bad fit of both equations (1) and (2) here. The feeding of *Rhizopertha* adults has been shown to be probably unimportant in reducing natality. The three assumptions of equations (2) thus correspond to the biological facts: with the degree of crowding which occurs in these populations the intra- and interspecific factors inhibiting growth are linearly related to population density during almost the whole of population growth, and the competitive relationship between the two species (α, β) and the potential rates of increase (b_1 and b_2), although fluctuating a good deal, undergo no systematic change. Furthermore, the limiting population of *Rhizopertha* has been shown to be independent of the initial population (vide supra). Now values of α and β may be estimated from the independent observations made on these species. *Rhizopertha* has three possible advantages over *Sitotroga*: (1) in larval competition, (2) as a result of the feeding, and (3) of the longevity of the adults. With the data available the values of α and β can be calculated only with reference to larval competition. Now when the larvae of each species alone were present in wheat grains the emerging adults were of course 100 % of this species. When half the larvae of one species were replaced by the same number of larvae of the other, the progeny then consisted of 43 % *Sitotroga* and 57 % *Rhizopertha* (Crombie 1944). Thus *Rhizopertha* inhibited *Sitotroga* by $57/50 = 1{\cdot}14$ times as much as the same number of the latter species, i.e. $\beta = 1{\cdot}14$. *Sitotroga* inhibited *Rhizopertha* by $43/50 = 0{\cdot}86$ time as much as the same number of the

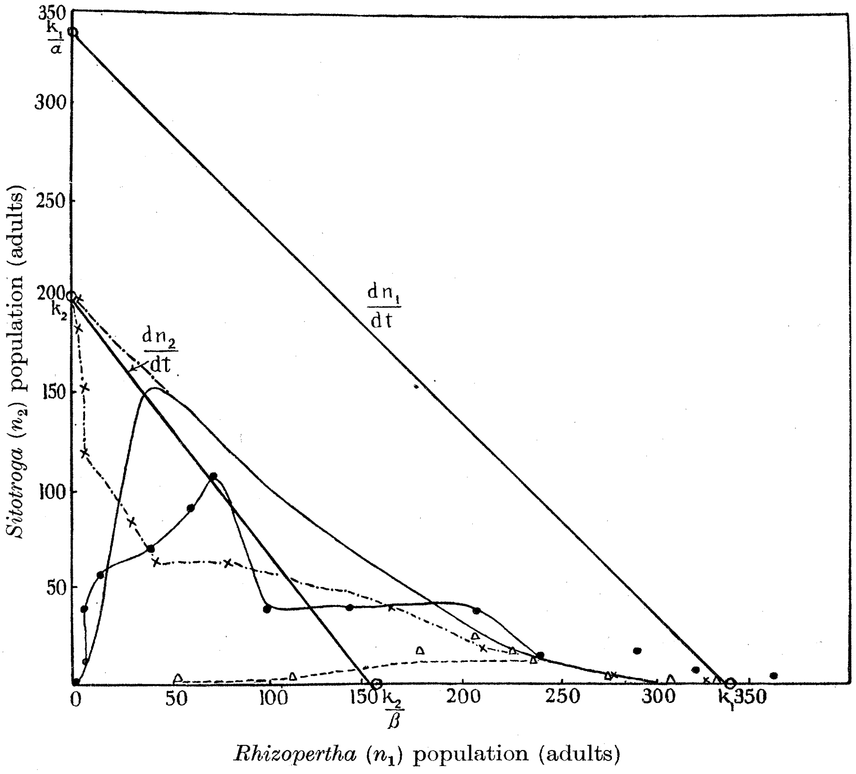

FIGURE 2. Diagram illustrating the competition between *Rhizopertha* (n_1) and *Sitotroga* (n_2) in renewed wheat, with different initial concentrations. Two *Rhizopertha* versus 2 *Sitotroga*: ●———● (observed, table 1*c*), ——— (calculated); 50 *Rhizopertha* versus 2 *Sitotroga*: △ (observed, table 2*e*), – – – – (calculated); 2 *Rhizopertha* versus 200 *Sitotroga*: × – • – • – × (observed, table 3*e*), – • – • – • (calculated) (cf. figure 1). The two broken theoretical curves eventually join the full theoretical curve.

$$dn_1/dt = k_1 - n_1 - \alpha n_2 = 0; \quad dn_2/dt = k_2 - n_2 - \beta n_1 = 0.$$

latter species, i.e. $\alpha = 0{\cdot}86$. These values satisfy the inequalities of the second condition of equilibrium for equations (2) and they fall well within the range of variation shown by the values calculated from the populations themselves (table 4). The closeness of these values of α and β to those calculated from equations (2) agrees with the conclusion already drawn from other evidence that by far the most important factor in interspecific competition is the struggle between larvae. The indices α and β thus chiefly represent this single factor. It may be concluded therefore that equations (2) may not only be used empirically to predict the most probable course of change in population size, but that each of the parameters may be given a biological meaning in virtue of which it really corresponds (although sometimes inaccurately) to a factor operating in nature.

4. THE COMPETITION OF *RHIZOPERTHA* AND *SITOTROGA* IN UNRENEWED MEDIA

Population counts were made once every 7 or 14 days as before, but the conditioned frass was not removed and no fresh wheat was added, so that with the passage of time the food supply was gradually used up and the medium became more and more conditioned. Certain other observations were also made at intervals. At each count the medium was weighed. Approximately every 42 days the fecundity of *Rhizopertha* females was measured: first, over a period of 4 days in part of the medium from the jar from which they had been taken; then in fresh flour to which the females were transferred. In the fresh flour observations were made every 4 days until fecundity had ceased to increase. The medium was obtained from the jars by sieving their contents. The experimental procedure was similar to that described in Crombie (1942, § IV). The fecundity of the females at intervals both in the increasingly conditioned and depleted medium in which they have been living and in fresh flour, and also the rate of recovery of the females after they have been transferred from the conditioned to fresh flour, were thus measured. The eggs oviposited, and the conditioned medium used, were replaced in the experimental jars.

Similar observations were made with *Sitotroga*. To obtain freshly emerged females from a particular jar all the living adults were removed from it to another jar. The latter contained strips of cardboard fastened together with paper clips so that the females could oviposit if necessary. The experimental jars were replaced in the incubator and the adults which had emerged overnight were removed for fecundity measurements. The main population of adults, with the eggs they may have oviposited, were then replaced in the experimental jars. This procedure was sometimes repeated for several days running if not enough new adults emerged. The fecundity of each of the freshly emerged females was then measured individually as described in Crombie (1942), one male being placed with each female. The eggs oviposited by the females were counted each day until oviposition ceased, when the females were killed, weighed, and length from head to wing tip measured. The eggs were replaced in the experimental jars from which the adults were taken.

These observations were made at intervals of approximately 42 days. Besides this, at every population count, the *Sitotroga* corpses were sexed, and the length from head to wing tip measured.

A number of experimental jars were set up with different initial numbers of *Rhizopertha* and *Sitotroga* as shown in table 5. There were two parallel jars for each experiment. When each species was alone the populations increased to maximum values and then declined and died out when the medium was exhausted (figure 3). The initial rate of increase of each species was approximately equal to that when the medium was renewed (table 1 *a, b*). The maximum population of *Rhizopertha* here was 267. The average weight of medium left per jar after the population had died out was 4 g. It consisted entirely of a brownish sour-smelling frass with a few husks. The maximum population reached by *Sitotroga* alone was 170, and an average of 4 g. per jar of wheat husks and frass were left after the population had died out. Now the first filial generation of *Sitotroga* adults reached a maximum at any time of 55. The actual number of individuals in this generation (between days 28 and 42) was 58. Approximately half of these were females so that they would lay about 3000 eggs (Crombie 1942). The second generation reached a maximum at any time of 170 and the number of individual adults which emerged in this generation (between days 63 and 84) was 174 or 0·87 per grain. The total number of individual adults produced by the 10 g. (200 grains) of wheat from the second generation onwards was 379 or 1·8 per grain. Why then, although the number of eggs present at the start of the second generation was far in excess of 379, was only 0·87 adult produced in the second generation per grain when the

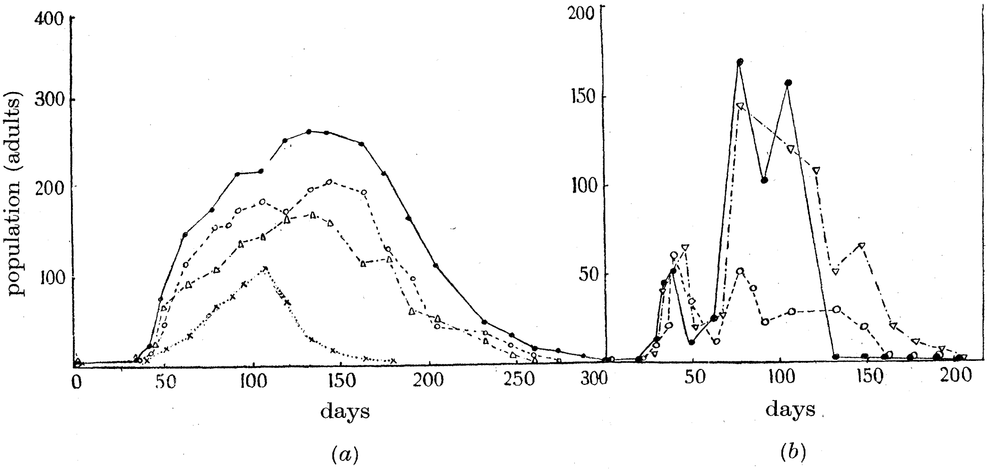

FIGURE 3. The growth of populations of (*a*) *Rhizopertha* and (*b*) *Sitotroga* in unrenewed medium. ●, separately (table 5 *a, b*); ○, 2 *Rhizopertha* versus 2 *Sitotroga* (table 5*c*); ×, (*a*) 2 *Rhizopertha* versus 150 *Sitotroga* (table 5*g*); △, ▽, 2 *Rhizopertha* and 2 *Sitotroga*, respectively, versus 2 *Oryzaephilus* (tables 8*b* and 7*d*) (cf. figure 8).

latter could actually support 1·8? The answer is presumably that active competition between the larvae for space prevented the full use of the food supply present (Crombie 1944). When they follow each other at a great enough interval, however, this competition is less severe so that successive generations were able to use the same grains until the latter were at length exhausted (after 437 adults or 2·19 per grain had emerged) and the population suddenly died out except for a few stragglers. At 18·5 mg. per insect 437 *Sitotroga* would consume 8·1 g. of wheat during development. Some of the remaining 1·9 g. would be consumed by larvae which succumbed before pupation, but it seems that most of these would have died in early instars before consuming much food (Crombie 1944), and evidence already published suggests that the food value of the medium was not exhausted even after the extinction of the population (Crombie 1942, § IV). The total number of *Rhizopertha* adults produced by 200 grains of wheat (i.e. the number of corpses counted) was 387 or 1·9 per grain. At the rate of 11·5 mg. per larva 4·45 g. wheat would have been consumed by these during development. Of the 5·55 g. remaining

TABLE 5. THE GROWTH OF POPULATIONS OF *RHIZOPERTHA* AND *SITOTROGA* IN WHEAT. MEDIUM *NOT* RENEWED

	(a)	(b)	(c)		(d)	
	Rhiz.	*Sit.*	2 *Rhiz.* v. 2 *Sit.*		50 *Rhiz.* v. 2 *Sit.*	
days	alone	alone	*Rhiz.*	*Sit.*	*Rhiz.*	*Sit.*
0	2	100 eggs	2	100 eggs	50	100 eggs
14	2	0	2	0	50	0
28	2	13	2	8	40	4
35	3	48	3	20	57	26
42	20	55	13	63	74	26
49	74	11	46	33	112	6
63	143	22	112	11	141	2
77	173	170	156	51	205	30
84	—	103	157	42	—	—
91	212	100	173	20	255	6
105	215	157	180	24	230	3
119	255	0	172	29	230	3
133	267	3	195	14	198	1
147	260	2	203	2	154	—
161	245	2	194	1	115	—
175	213	1	135	1	66	—
189	162	2	98	0	39	—
203	111	0	45	1	26	—
231	47	0	38	—	13	—
245	31	0	18	—	6	—
259	16	—	9	—	1	—
273	12	—	2	—	0	—
287	7	—	0	—	—	—
301	3	—	—	—	—	—
315	0	—	—	—	—	—
total number individuals	387	437	263	120	325	55

out of the original 10 g. some would have been consumed by the 387 adults, some by the larvae which succumbed before pupating, and the balance is made up of the part which remained after the extinction of the population (Crombie 1942, § IV). The amount eaten by the latter is believed (as with *Sitotroga*) to be small (Crombie 1944). The overlapping of generations prevents the estimation of the size of each generation of this species. The average longevity of *Rhizopertha* adults in unrenewed medium was 106 (65–146 days). This value underwent no regular change with time (i.e. population density). A *t*-test revealed that longevity here was significantly lower than that (159 days) in renewed media ($p < 0{\cdot}01$).

TABLE 5 (*contd.*)

	(*e*) 250 *Rhiz.* v. 2 *Sit.*		(*f*) 2 *Rhiz.* v. 50 *Sit.*		(*g*) 2 *Rhiz.* v. 150 *Sit.*	
days	*Rhiz.*	*Sit.*	*Rhiz.*	*Sit.*	*Rhiz.*	*Sit.*
0	250	100 eggs	2	2500 eggs	2	7500 eggs
14	210	0	0	0	2	0
28	200	0	0	0	2	0
35	216	0	12	126	2	0
42	274	3	27	117	5	90
49	269	27	59	19	15	220
63	165	5	76	46	30	50
77	180	6	75	168	68	75
84	—	—	—	—	—	—
91	145	1	86	112	80	28
105	135	1	98	17	90	11
119	104	1	116	5	102	3
133	70	—	103	1	70	0
147	39	—	105	1	27	1
161	24	—	63	—	12	—
175	4	—	39	—	6	—
189	0	—	15	—	1	—
203	—	—	4	—	0	—
231	—	—	0	—	—	—
245	—	—	—	—	—	—
259	—	—	—	—	—	—
273	—	—	—	—	—	—
287	—	—	—	—	—	—
301	—	—	—	—	—	—
315	—	—	—	—	—	—
total number individuals	315	42	157	368	127	288

When the two species were competing the *Sitotroga* always died out first. With initially two of each species per jar (table 5*c*) only 0·28 *Sitotroga* individuals emerged per grain in the second generation (between days 63 and 84). During approximately the same period (days 49–84) 0·55 *Rhizopertha* adults had emerged per grain. When one species was initially inferior to the other the amount of increase it was able to achieve decreased in proportion to the initial numbers of the originally superior species. The numbers of individual adults (i.e. corpses) in each population are shown at the foot of table 5. When the numbers of each species are plotted against each other there is seen to be a linear relationship between them (figure 4). One *Rhizopertha* occupies the space in the environment of 1·18 *Sitotroga* and one *Sitotroga* that of 0·85 *Rhizopertha*.

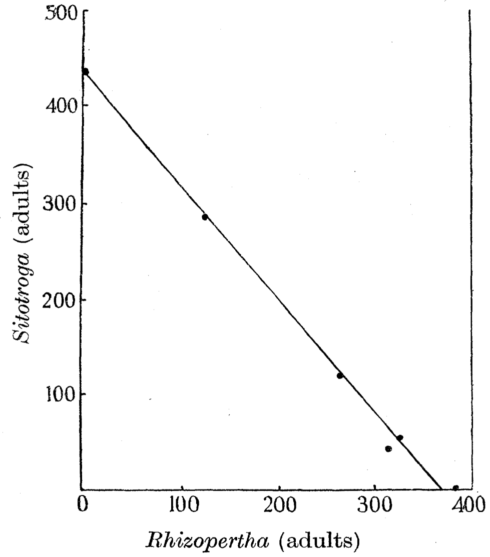

FIGURE 4. The relationship between the total number of individual adults (i.e. corpses counted) of *Rhizopertha* and *Sitotroga* which emerged from 10 g. of wheat (unrenewed) with different initial concentrations of the two species (table 5).

The changes observed in the fecundity of *Rhizopertha* followed the same course in all the experiments, so that only data from the population shown in table 5*a* need be given. Each value for fecundity in table 6 is the average of observations with twenty-four females up to the 210th day, and thereafter with not less than four females. With the passage of time the weight of the medium decreased, the fecundity of the females decreased, and the time taken for the latter to recover in fresh flour increased. The females were considered as having recovered when fecundity ceased to rise in fresh flour, observations being made every 4 days. As conditioning became heavier its effects became more severe (cf. Crombie 1942). After the 210th day the females seem to have been permanently affected, fecundity remaining at a low value in fresh flour. But the number of females here was rather small. Now the *Rhizopertha* population began to die out between the 119th and the 161st day, but oviposition did not cease until the 252nd day, although it had practically ceased by the 210th day. The decrease in natality which led to the dying out of the population must therefore have been due to larval mortality, not to cessation of oviposition of the existing adult females. The average longevity of the *Rhizopertha* adults was unaffected by the competition of *Sitotroga* except in table 5*g*, when it was 67 (35–97) days. A *t*-test shows that this is significantly lower than the longevity (106 days) when *Rhizopertha* was alone ($0.02 < p < 0.05$). The reason for this may be that the high initial *Sitotroga* population rapidly used up the medium thus reducing the belated *Rhizopertha* adults to starvation.

TABLE 6. CHANGES IN FECUNDITY OF *RHIZOPERTHA* IN UNRENEWED MEDIA WITH TIME

time in days	weight of medium remaining g.	fecundity of *Rhiz.* in (a) conditioned medium	(b) fresh flour	time for recovery in (b) days
48	8·9	4·9	8·7	4
84	6·0	3·7	7·9	4
126	5·5	2·35	11·2	8
168	5·0	1·8	7·7	8
210	4·6	0·13	9·2	12
252	4·2	0	3·2	12
294	4·0	0	3·2	16

The average lengths (from proboscis to wing tip) of the dead *Sitotroga* which had been reared in renewed medium were 5·51 mm. for females and 4·88 mm. for males. These values were significantly different (t corresponded to $p = 0.02$). The average lengths of dead adults from unrenewed media were ♀ = 4·62 mm. and ♂ = 4·24 mm. There was no significant difference between these two figures, but the members of each sex, respectively, were significantly smaller than they were in renewed media ($p = 0.02$). In unrenewed media the average length gradually decreased with time (from days 56–203) from 3·6–2·25 mm. for females and from 4·04–2·25 mm. for males ($p < 0.05$). There was no such decrease in renewed media. In renewed media the average weight of females was 3·7 mg. and of males 1·8 mg. The average total number of eggs laid by the former was 119. There appears to have been a gradual decline in the average weight and fecundity of insects from unrenewed media after about day 56, but variability was great and the numbers involved were too small for significant differences to be established. When populations were dying out a few 'midgets' usually appeared. Female midgets weighed about 0·9 mg. and laid about 8 eggs (cf. Simmons & Ellington 1933). The longevity of *Sitotroga* adults was apparently unaffected by being reared in unrenewed medium. The sex ratio remained at approximately unity in both media.

5. THE COMPETITION OF *RHIZOPERTHA* AND OF *SITOTROGA* WITH *ORYZAEPHILUS*

(*a*) *Competition of* Sitotroga (n_1) *and* Oryzaephilus (n_2). There were two sets of experiments: in the first the medium was renewed as described above; in the second the medium was not renewed. There were two parallel jars for each experiment. The wheat was more deeply cracked than before to enable the *Oryzaephilus* to attack it. The results are given in table 7 and figure 5. When the two species were competing each rose to a maximum population at which it continued until the end of the experiment. Neither drove out the other. The maximum population for *Sitotroga* was approximately 153 as compared to 200 when it was living alone (table 1*b*). Figure 5*a* shows that the generation maxima occurred after approximately the same periods as in table 1*b*. *Oryzaephilus* reached a maximum population of approximately the same value (445) when competing with *Sitotroga* as it did when living alone. As already mentioned, this is to be expected since *Sitotroga* adults do not feed and the larvae live and feed inside the grains, by which they are protected, while *Oryzaephilus* larvae and adults live and feed outside the grains. Each species therefore occupies an entirely different ecological niche.

TABLE 7. THE GROWTH OF POPULATIONS OF *SITOTROGA* AND *ORYZAEPHILUS* IN WHEAT. (MEDIUM RENEWED IN *a* AND *c*)

days	(*a*) *Oryz.* alone	(*b*) *Oryz.* alone (medium *not* renewed)	(*c*) 2 *Sit.* v. 2 *Oryz.*		(*d*) 2 *Sit.* v. 2 *Oryz.* (medium *not* renewed)	
			Sit.	*Oryz.*	*Sit.*	*Oryz.*
0	4	2	100 eggs	2	100 eggs	2
14	4	2	0	2	0	2
28	4	14	0	12	0	14
35	25	52	46	27	44	32
42	44	69	58	31	67	51
49	63	79	10 (88)	38	15	64
63	147	111	18 (125)	73	27	78
77	285	120	153	146	147	202
84	—	—	53 (153)	—	32	236
91	345	125	118 (153)	258	22	250
105	361	178	158 (153)	340	118	213
119	405	215	110	320	104	223
133	471	298	36	435	50	201
147	420	305	146	460	66	168
161	430	290	20	395	18	128
175	420	—	—	—	12	93
189	475	260	179	468	4	71
203	435	260	127	482	0	60
231	480	266	58	420	0	40
259	—	24	150	421	0	15
287	—	3	—	—	—	4
315	—	0	—	—	—	0

The logistic equation fitted to the data in column (*a*) is shown in figure 5*b*: $k_2 = 445$ and $b_2 = 0{\cdot}07$. Points on the *Sitotroga* curve between generation maxima were smoothed as before and are given in brackets in the table. The values of α and β calculated with equations (2) from the competing populations after they had reached their maxima were $\alpha = 0{\cdot}1$ and $\beta = 0$. These values were used when calculating b_1 and b_2. The average values of these indices were $b_1 = 0{\cdot}07$ (0·041–0·12) and $b_2 = 0{\cdot}054$ (0·027–0·067) during the periods of days 35–77 and 35–105, respectively. The figures in brackets show the range of fluctuation. There was no regular change in value with time. The values of α and β were calculated at the same points with $b_1 = 0{\cdot}1$ and $b_2 = 0{\cdot}07$. The average values of these indices were $\alpha = 0{\cdot}29$ ($0{\cdot}1$–$0{\cdot}52$) and $\beta = 0{\cdot}097$ ($-0{\cdot}05$–$0{\cdot}32$) during the period of days 63–133 and at the maxima. Both indices tended to decrease with time over the ranges shown in brackets. Now $k_1/k_2 = 200/445 = 0{\cdot}45$ and $k_2/k_1 = 445/200 = 2{\cdot}225$. Except that on day 63 $\alpha = 0{\cdot}52$, the inequalities $\alpha < k_1/k_2$ and $\beta < k_2/k_1$ (or $\alpha/k_1 < 1/k_2$ and $\beta/k_2 < 1/k_1$) are therefore always satisfied from this day onwards. These inequalities correspond to the first condition of equilibrium for equations (2) in which both species continue to exist together. Equations (2) were fitted to the data in table 7*c* with $b_1 = 0{\cdot}1$, $b_2 = 0{\cdot}07$, $\alpha = 0{\cdot}1$ and $\beta = 0$ (see figure 5).

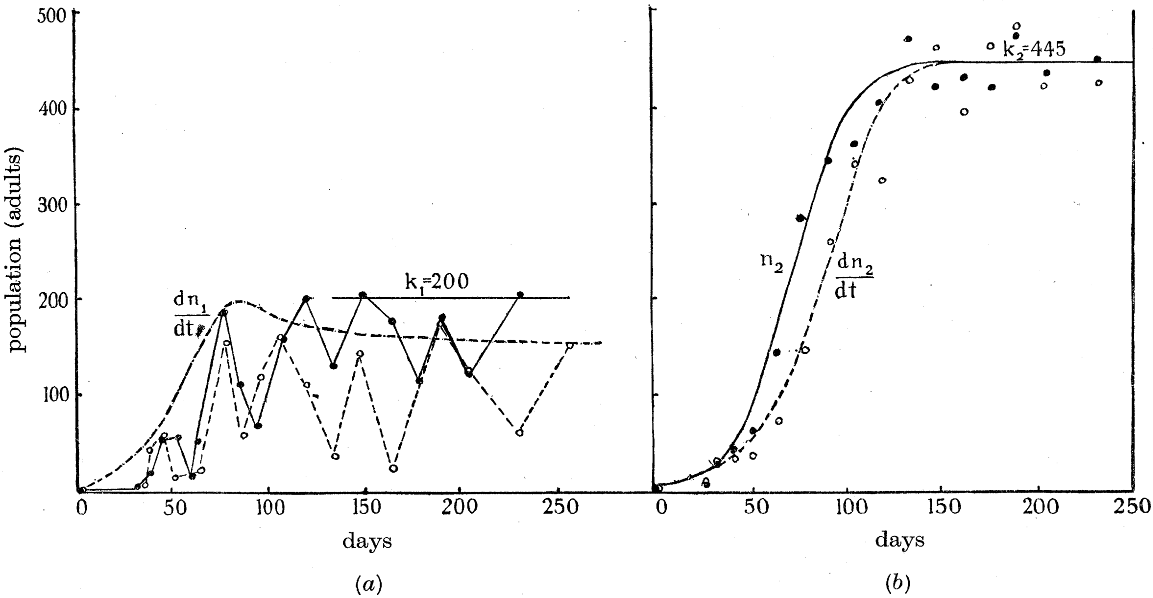

FIGURE 5. The growth of populations of (*a*) *Sitotroga* (n_1) and (*b*) *Oryzaephilus* (n_2) in renewed wheat. ●, separately (tables 1*b* and 7*a*); ○, in competition (table 7*c*). The smooth lines represent the calculated curves.

$dn_1/dt = 0{\cdot}1n_1(200 - n_1 - 0{\cdot}1n_2)/200$; $n_2 = 445/(1 + 163e^{-0{\cdot}07t})$; $dn_2/dt = 0{\cdot}07n_2(445 - n_2)/445$.

The average longevity of *Oryzaephilus* adults in renewed medium (table 7*a*) was 90 (56–137) days. The average rate of adult mortality in the maximum population was 0·0036 (0·00076–0·0057) per adult per day. Now in this population there were 2·25 beetles per grain, and at this density the fecundity of this species is approximately 0·7 egg per adult per day (Crombie 1942). Therefore about 99·48 % of the eggs died in the immature stages and only 0·52 % went to produce new adults. The average adult longevity was not significantly different from 90 days either in unrenewed medium or when this species was in competition with *Sitotroga*. In neither medium did adult longevity change regularly with time (i.e. density). In table 7*b* the adult population rose to a maximum of 305 and died out suddenly after the 231st day. At the end of this time the average weight of medium left per jar was 3·7 g. The total number of adults (i.e. corpses) produced by 200 grains was 541 or 2·7 per grain. At 6·57 mg. per larva (Crombie 1943*b*) these would consume 3·65 g. during development, leaving 6·35 g. to the adults, unsuccessful larvae and residual food left after the extinction of the population (Crombie 1942, § IV). Now *Oryzaephilus* females will oviposit in a medium in which a population has died out (Crombie 1943*b*), so that the eventual extinction of the population here must have been due to the failure of larvae to survive in such a medium (after about day 147), followed by the death of the existing adults from old age (cf. Park 1938).

When the two species were competing in unrenewed medium (table 7*d*; figures 3, 8) the total number of *Sitotroga* individual adults which emerged was 402 or 2·01 per grain as compared with 2·19 per grain when this species was living alone (table 5). The presence of *Oryzaephilus* therefore hardly affected the opportunity for increase of *Sitotroga*. But the total number of *Oryzaephilus* individual adults was reduced from 541 to 301, or only 1·5 per grain. Therefore in competition one *Sitotroga* occupies the space in the environment of (514–301)/402 = 0·53 *Oryzaephilus*, and one *Oryzaephilus* that of only (437–402)/307 = 0·12 *Sitotroga*. The explanation of these results is perhaps that the *Sitotroga* larvae inside the grains were able to develop almost unmolested by the *Oryzaephilus* which feed outside. When the

TABLE 8. THE GROWTH OF POPULATIONS OF *RHIZOPERTHA* AND *ORYZAEPHILUS* IN WHEAT. (MEDIUM RENEWED IN *a*, *c* AND *d*)

	(*a*) 2 *Rhiz.* v. 2 *Oryz.*		(*b*) 2 *Rhiz.* v. 2 *Oryz.* (medium *not* renewed)		(*c*) 50 *Rhiz.* v. 2 *Oryz.*		(*d*) 2 *Rhiz.* v. 100 *Oryz.*	
days	*Rhiz.*	*Oryz.*	*Rhiz.*	*Oryz.*	*Rhiz.*	*Oryz.*	*Rhiz.*	*Oryz.*
0	2	2	2	2	50	2	2	100
14	2	2	2	2	50	2	2	100
28	2	4	2	10	50	2	2	100
35	2	33	2	36	48	33	2	330
42	21	41	23	51	101	41	3	357
49	59	53	61	60	152	58	8	360
63	116	74	90	86	215	105	19	390
77	120	127	105	152	229	155	38	415
91	138	190	133	207	270	225	83	415
105	152	203	140	209	290	275	130	545
119	193	305	160	295	265	340	138	540
133	260	385	168	293	265	310	150	550
147	255	480	155	239	285	350	145	500
161	245	405	116	110	295	340	157	490
175	250	425	120	13	280	370	225	450
189	260	425	61	9	255	375	287	430
203	210	450	51	6	265	430	242	410
231	233	413	27	3	290	415	281	405
259	255	425	10	1	280	400	240	420
273	260	415	2	0	—	—	—	—
287	260	420	—	—	—	—	—	—

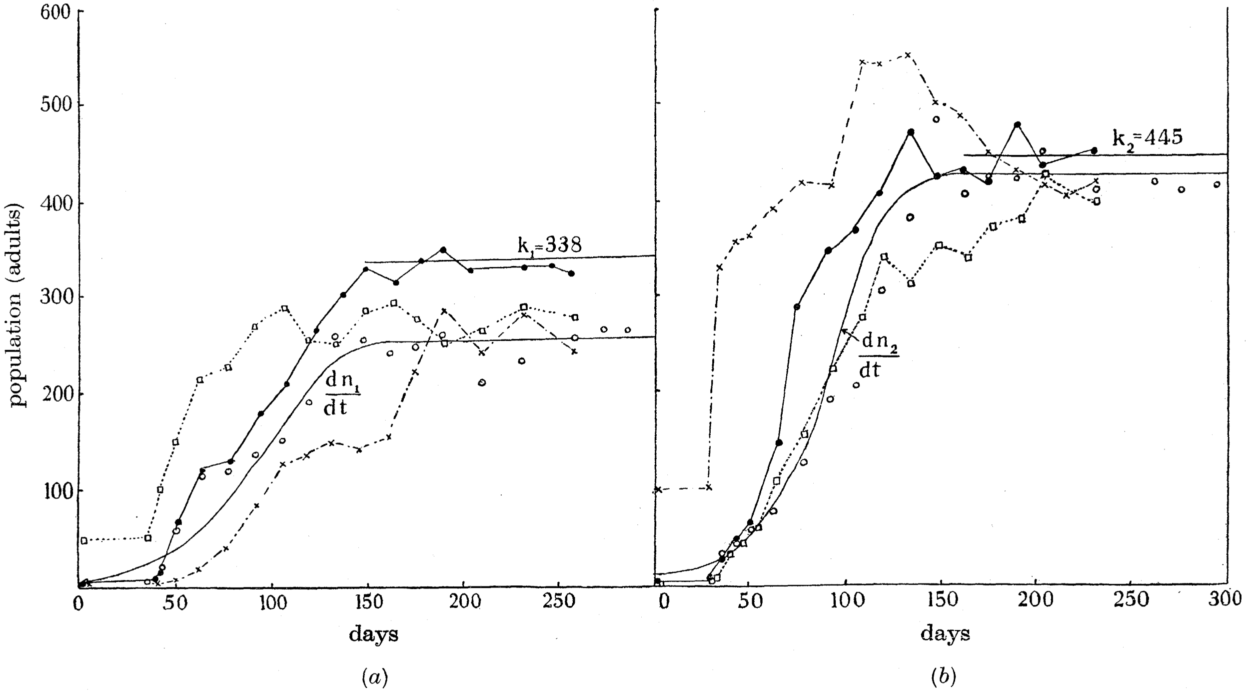

FIGURE 6. The growth of populations of (*a*) *Rhizopertha* (n_1) and (*b*) *Oryzaephilus* (n_2) in renewed wheat. ●, separately (tables 1*a* and 7*a*); ○, 2 *Rhizopertha* versus 2 *Oryzaephilus* (table 8*a*); □, 50 *Rhizopertha* versus 2 *Oryzaephilus* (table 8*c*); ×, 2 *Rhizopertha* versus 100 *Oryzaephilus* (table 8*d*). The smooth lines represent the curves calculated for table 8*a*.

$$dn_1/dt = 0{\cdot}05n_1(338 - n_1 - 0{\cdot}2n_2)/338; \quad dn_2/dt = 0{\cdot}07n_2(445 - n_2 - 0{\cdot}1n_1)/445.$$

latter had eaten into the grains, however, they found that the interior had been consumed by the developing *Sitotroga*. The amount of food remaining for the *Oryzaephilus* was thus reduced by the presence of the *Sitotroga*, while the larvae of the latter species were able to make use of the grains as long as the mechanical properties of the latter remained suitable for their development. Thus here *Sitotroga* is in better position than *Oryzaephilus* to make use of the limited food supply. When the medium was renewed and food plentiful the main factor in competition was probably the predaceous habits of the *Oryzaephilus* adults and larvae which gave a slight advantage to this species (Crombie 1943 *b*).

(*b*) *Competition of* Rhizopertha (n_1) *and* Oryzaephilus (n_2). When the medium was renewed the population of each species rose to a maximum and continued there (table 8, figure 6). These maxima (approximately 250 for *Rhizopertha* and 429 for *Oryzaephilus*) were the same whether the initial populations of each species were equal or unequal. There is thus a condition of equilibrium at which both species can exist together. This is to be expected since as already mentioned the two species occupy different ecological niches. The larvae of *Rhizopertha* feed inside the grains whereas adults and larvae of *Oryzaephilus* feed outside. The latter species would therefore come into competition only with the *Rhizopertha* adults which may feed outside the grains.

TABLE 9. AVERAGE VALUES OF α, β, b_1 AND b_2 DURING THE COMPETITION OF *RHIZOPERTHA* (n_1) AND *ORYZAEPHILUS* (n_2)

table	range of days	α $(b_1 = 0{\cdot}05)$	β $(b_2 = 0{\cdot}07)$
10*a*	42–133	0·6 (0·05–1·37)	0·51 (0·05–1·27)
10*b*	42–119	0·14 (–0·32–0·35)	0·49 (0·14–1·23)
10*c*	63–175	0·1 (–0·25–0·36)	0·04 (–0·7–1·21)

table	range of days	b_1 $(\alpha = 0{\cdot}2)$	b_2 $(\beta = 0{\cdot}1)$
10*a*	42–133	0·092 (0·03–0·29)	0·068 (0·04–0·079)
10*b*	42–119	0·051 (0·023–0·109)	0·049 (0·39–0·067)
10*c*	63–175	0·051 (0·019–0·094)	0·046 (–0·03–0·225)

The values of α and β when the competing populations had reached their maxima were $\alpha = 0{\cdot}2$ and $\beta = 0{\cdot}1$. These values were used in calculating b_1 and b_2 at points in the middle region of population growth. The values of the latter indices derived from the fitting of logistic curves ($b_1 = 0{\cdot}05$, $b_2 = 0{\cdot}07$) were used in calculating α and β at the same points. The periods of days over which these calculations were made are shown in table 9. Widely divergent values which sometimes appeared at the beginning and end of population growth were omitted when calculating the average values of α, β, b_1 and b_2. These indices underwent no regular change in value with time except in table 8*a*, where α and β were both rather large at first and then gradually decreased. Equations (2) were fitted to the experimental data in table 8 *a*, *c* and *d* with $b_1 = 0{\cdot}05$, $b_2 = 0{\cdot}07$, $\alpha = 0{\cdot}2$ and $\beta = 0{\cdot}1$ (figures 6, 7). The fit is not very accurate but sufficiently so to satisfy the inequalities $\alpha < k_1/k_2$ and $\beta < k_2/k_1$, where $k_1/k_2 = 338/445 = 0{\cdot}76$ and $k_2/k_1 = 445/338 = 1{\cdot}32$. These inequalities correspond to the first condition of equilibrium for equations (2). In figure 7 n_1 is plotted against n_2. The turning points occur near the straight lines connecting points where dn_1/dt and dn_2/dt, respectively, are zero, and the curves migrate to the intersection of these two lines.

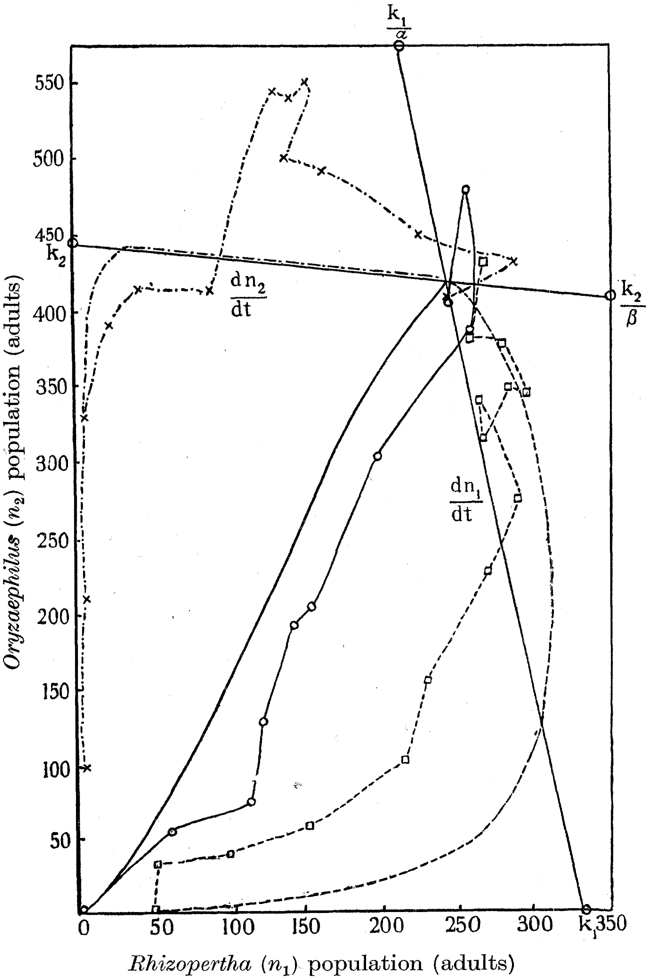

FIGURE 7. Diagram illustrating the competition between *Rhizopertha* (n_1) and *Oryzaephilus* (n_2) in renewed wheat, with different initial concentrations. Two *Rhizopertha* versus 2 *Oryzaephilus*: ○———○ (observed, table 8*a*), ——— (calculated); 50 *Rhizopertha* versus 2 *Oryzaephilus*: □---□ (observed, table 8*c*), --- (calculated); 2 *Rhizopertha* versus 100 *Oryzaephilus*: ×—·—·—·× (observed, table 8*d*), —·—·—· (calculated) (cf. figure 6).

$$dn_1/dt = k_1 - n_1 - \alpha n_2 = 0; \quad dn_2/dt = k_2 - n_2 - \beta n_1 = 0.$$

The longevity of neither species was affected by competition with the other in either renewed or unrenewed media. The 10 g. of unrenewed medium (table 8*b*; figures 3, 8) produced 250 *Rhizopertha* and 315 *Oryzaephilus* individual adults. Therefore in competition one *Rhizopertha* occupies the space in the environment of (514–315)/250 = 0·8 *Oryzaephilus* and one *Oryzaephilus* that of (387–250)/315 = 0·44 *Rhizopertha*. The competitive relationship has thus shifted slightly in favour of *Rhizopertha* as compared with that in renewed medium.

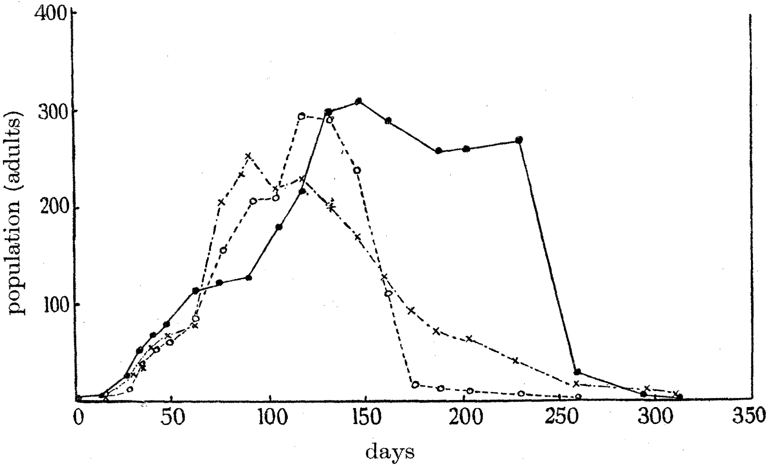

FIGURE 8. The growth of populations of *Oryzaephilus* in unrenewed wheat. ●, separately (table 7*b*); ×, competing with *Sitotroga* (table 7*d*); ○, competing with *Rhizopertha* (table 8*b*) (cf. figure 3).

6. DISCUSSION

The four equilibrium conditions of equation (2) depend only on the competitive relationship between the two species. The first equilibrium condition would be reached between species with different needs or habits and the second or third between those with identical needs and habits, i.e. species which occupy the same ecological niche. Thus either *Rhizopertha* or *Sitotroga* could survive in the same environment as *Oryzaephilus* but could not survive together. Theoretically, equilibrium should be stable, i.e. it should be maintained only at a certain concentration of each species to which the populations return if they are displaced to any other values. This occurred in populations of these insects, and it has also been observed by Gause (1935, 1937) in some Protozoa, although not in others (Gause & Witt 1935). But as Gause (1934, 1939) has pointed out, such stability must be an important factor regulating the composition of biotic communities, in which the continuous process of competition automatically leads to the re-establishment of the stable state if it is disturbed (Carpenter 1939; Garrett 1939; Clements & Shelford 1939). Independent research into the intra- and interspecific factors inhibiting increase showed that within the relevant regions of population growth the biological assumptions on which equations (1) and (2) are based were true for populations of *Rhizopertha* and *Sitotroga* under the environmental conditions defined above. All the parameters could therefore be given biological meaning. Because of fluctuations in the value of these coefficients, equations (2) sometimes do not give a very good fit when they are fitted to all the observed points at once, but they were always successful in predicting the outcome of competition. But unless their biological assumptions are shown to be true of particular organisms under specific environmental conditions such equations can only be regarded as empirical expressions incapable of yielding biological deductions, even though, as Park (1939) has pointed out, they may be useful demographic instruments. Hotelling (1927) suggests that as an empirical equation (1) may be used to give the most probable value of the relative rate of increase of the population *at any moment*, and the same may go for equations (2).

It is easy to demonstrate theoretically that two species with identical ecological niches cannot survive together in the same environment unless density-independent factors keep the population low enough to eliminate interspecific competition (Clements & Shelford 1939, p. 175; Gause 1934, 1939; Crombie 1943 *b*). This must restrict the population density and distribution of many species in nature. For instance, Clements, Weaver & Hanson (1929) observed that competition was keenest between plants which were similar in vegetation and form. A very dissimilar plant could enter a community without competition, while an invader more like those forming the community was excluded. D'Aeth (1939) and Nicol & Thornton (1941) found a similar situation in fungi and in root nodule bacteria, respectively. Carpenter (1940) found that fluctuations of insect populations in Europe are a general phenomenon of a large area. Very often concurrently outbreaking species fall into the same ecological niche. In subsequent outbreaks in the same area the same species may not always take the lead, but one of the former subordinate species may take the place of greatest abundance (cf. Winsor 1934). The distribution of some fresh-water triclads in mountain streams is restricted by the competition of other species with similar habits as well as by environmental conditions such as temperature and rate of flow of water. Each species has an optimum region from which it usually keeps out the others, although when only one species is present it may occupy a much larger stretch of stream (Beauchamp & Ullyott 1932; cf. Lloyd, Graham & Reynoldson 1940). It seems probable that more detailed knowledge will reveal that nearly related forms of organisms (of specific or below specific rank) which occupy the same area never occupy exactly the same ecological niche unless, as mentioned above, density-independent factors prevent competition (cf. Lack 1940*a*, *b*; Diver 1939; Hogben 1940; Dobzhansky 1941, ch. 6; Huxley 1942, chs. 5, 6; Mayr 1942). This is likely to lead to speciation when genetic divergence separates one interfertile group into two (Huxley 1942, p. 328). Each group is likely to occupy a sharply defined section of the environment (to which it is better adapted than the other) from which the other is excluded.

The competitive relationship between *Oryzaephilus* and *Rhizopertha* or *Sitotroga* changed slightly in favour of the latter species in unrenewed as compared with renewed media. This principle, that the results of competition between different organisms may vary with the conditions under which it occurs (Huxley 1942, p. 119), is very important in ecological succession. It has often been observed that the dominant type at a given period gradually alters the environmental conditions in favour of another type which then ousts its predecessor by competition (Fuller 1934; Gause 1936; Hutchinson 1941).

I should like to thank Dr A. D. Imms, F.R.S., and Dr W. H. Thorpe for their general interest and advice, Dr J. H. Sang for kindly allowing me to read in manuscript work covering similar ground, and Dr O. W. Richards for supplying the original insects from Imperial College Field Station, Slough.

References

Allee, W. C. 1934 *Biol. Rev.* **9**, 1.
Beauchamp, R. S. A. & Ullyott, P. 1932 *J. Ecol.* **20**, 200.
Bernstein, F. 1934 *Cold Spr. Harb. Symp. Quant. Biol.* **2**, 209.
Bodenheimer, F. S. 1938 *Problems of animal ecology.* Oxford.
Bowley, A. L. 1925 *J. R. Statist. Soc.* **88**, 76.
Carpenter, J. R. 1939 *Amer. Midl. Nat.* **21**, 75.
Carpenter, J. R. 1940 *J. Anim. Ecol.* **9**, 108.
Chapman, R. N. 1928 *Ecology,* **9**, 111.
Chapman, R. N. 1931 *Animal ecology.* New York: McGraw Hill.
Chapman, R. N. 1939 *Ecol. Monogr.* **9**, 261.
Clements, F. E. & Shelford, V. E. 1939 *Bio-ecology.* New York: Wiley.
Clements, F. E., Weaver, J. E. & Hanson, H. C. 1929 *Plant competition.* Washington: Carnegie Inst.
Crombie, A. C. 1942 *J. Exp. Biol.* **19**, 311.
Crombie, A. C. 1943*a* *Nature, Lond.,* **152**, 246.
Crombie, A. C. 1943*b* *Proc. Zool. Soc. Lond.* A, **113**, 77.
Crombie, A. C. 1944 *J. Exp. Biol.* **20**, 135.
D'Aeth, H. R. X. 1939 *Biol. Rev.* **14**, 105.
Darwin, C. 1859 *The origin of species.* London: John Murray.
Diver, C. 1939 *The new systematics*, p. 303, ed. J. Huxley. Oxford.
Dobzhansky, Th. 1941 *Genetics and the origin of species.* Columbia.
Elton, C. S. 1927 *Animal ecology.* London: Sidgwick and Jackson.
Fuller, M. E. 1934 *Bull. Coun. Sci. Industr. Res.* no. 82.
Garrett, S. D. 1939 *Tech. Commun. Imp. Soil Sci. Harpenden,* no. 38.
Gause, G. F. 1931 *Amer. Nat.* **65**, 70.
Gause, G. F. 1934 *The struggle for existence.* Baltimore: Williams and Wilkins.
Gause, G. F. 1935 Vérifications expérimentales de la théorie mathématique de la lutte pour la vie. *Act. Sci. et Ind.* no. 277. Paris: Hermann.
Gause, G. F. 1936 *Quart. Rev. Biol.* **11**, 320.
Gause, G. F. 1937 *Ecology,* **18**, 173.
Gause, G. F. 1939 *Amer. Midl. Nat.* **21**, 255.
Gause, G. F. & Witt, A. A. 1935 *Amer. Nat.* **69**, 596.
Graham, S. A. 1939 *Ecol. Monogr.* **9**, 301.
Gray, J. 1929 *Brit. J. Exp. Biol.* **6**, 248.
Hall, R. P. 1941 *Amer. Nat.* **75**, 419.
Harding, D. P. 1937*a* *J. Exp. Biol.* **14**, 422.
Harding, D. P. 1937*b* *J. Exp. Biol.* **14**, 431.

Hogben, L. T. 1931 *Biol. Rev.* **6**, 163.

Hogben, L. T. 1940 *The new systematics.* Ed. J. S. Huxley. Oxford.

Hotelling, H. G. 1927 *J. Amer. Statist. Ass.* **22**, 283.

Hutchinson, G. E. 1941 *Amer. Nat.* **75**, 406.

Huxley, J. S. 1942 *Evolution. The modern synthesis.* London: Unwin and Allen.

Jackson, C. H. N. 1936 *Proc. Zool. Soc. Lond.* p. 811.

Jahn, T. L. 1934 *Cold Spr. Harb. Symp. Quant. Biol.* **2**, 167.

Kavanagh, A. J. & Richards, O. W. 1934 *Amer. Nat.* **68**, 54.

Kostitzin, V. A. 1937 *Biologie Mathématique.* Paris: Armand Colin.

Lack, D. 1940*a* *Brit. Birds*, **34**, 80.

Lack, D. 1940*b* *Nature, Lond.*, **146**, 324.

Lloyd, Ll., Graham, J. F. & Reynoldson, T. B. 1940 *Ann. Appl. Biol.* **27**, 122.

Lotka, A. J. 1925 *The elements of physical biology.* Baltimore: Williams and Wilkins.

Lotka, A. J. 1932 *J. Wash. Acad. Sci.* **22**, 461.

Lotka, A. J. 1939 Théorie analytique des associations biologiques. *Act. Sci. et Ind.* no. 780. Paris: Hermann.

MacLagan, D. S. & Dunn, E. 1935 *Proc. Roy. Soc. Edinb.* **55**, 126.

Mayr, E. 1942 *Systematics and the origin of species.* New York: Columbia.

Medawar, P. B. 1941 *Nature, Lond.*, **148**, 772.

Nicol, H. & Thornton, H. G. 1941 *Proc. Roy. Soc.* B, **130**, 32.

Park, T. 1938 *Amer. Nat.* **72**, 24.

Park, T. 1939 *Amer. Midl. Nat.* **21** (1), 235.

Park, T., Gregg, E. V. & Lutherman, C. Z. 1941 *Physiol. Zoöl.* **14**, 395.

Pearl, R. 1924 *Studies in human biology.* Baltimore: Williams and Wilkins.

Pearl, R. 1925 *The biology of population growth.* New York: Knopf.

Pearl, R. 1927 *Quart. Rev. Biol.* **2**, 532.

Pearl, R. 1937 *Amer. Nat.* **71**, 50.

Pearl, R. & Reed, L. J. 1920 *Proc. Nat. Acad. Sci., Wash.*, **6**, 275.

Reed, L. J. & Berkson, J. 1929 *J. Phys. Chem.* **33**, 760.

Rhodes, E. C. 1937 *Act. Sci. et Ind.* no. 710, p. 40. Paris: Hermann.

Rhodes, E. C. 1940 *J. R. Statist. Soc.* **103**, 61, 218, 362 and 380.

Richards, O. W. 1934 *Cold Spr. Harb. Symp. Quant. Biol.* **2**, 157.

Salt, G. 1932 *Bull. Ent. Res.* **23**, 235.

Salt, G. 1940 *Biol. Rev.* **16**, 239.

Severtzoff, S. A. 1934 *Quart. Rev. Biol.* **9**, 409.

Smith, H. S. 1935 *J. Econ. Ent.* **28**, 873.

Simmons, P. & Ellington, G. W. 1933 *Tech. Bull. U.S. Dep. Agric.* **1**, 351.

Teissier, G. 1928 *Ann. Physiol. Physiochim. biol.* **4**, 342.

Teissier, G. 1937 Les lois quantitatives de la croissance. *Act. Sci. et Ind.* no. **455**. Paris: Hermann.

Thompson, Sir D'Arcy W. 1942 *On growth and form.* Cambridge.

Thompson, W. R. 1931 *Bull. Ent. Res.* **22**, 147.

Thompson, W. R. 1939 *Parasitology*, **31**, 299.

Volterra, V. 1926 *Mem. Accad. Lincei*, **2**, 31 (translation as appendix to Chapman 1931).

Volterra, V. 1931 *Leçons sur la théorie mathématique de la lutte pour la vie.* Paris: Gauthier-Villars.

Volterra, V. & D'Ancona, U. 1935 Les associations biologiques au point de vue mathématique. *Act. Sci. et Ind.* no. 243. Paris: Hermann.

Wilder, J. 1940 *Physiol. Zoöl.* **13**, 439.

Wilson, E. B. 1934 *Cold Spr. Harb. Symp. Quant. Biol.* **2**, 199.

Wilson, E. B. & Puffer, R. R. 1933 *Proc. Amer. Acad. Arts. Sci.* **68**, 285.

Winsor, C. P. 1932*a* *J. Wash. Acad. Sci.* **22**, 73.

Winsor, C. P. 1932*b* *Proc. Nat. Acad. Sci., Wash.*, **18**, 1.

Winsor, C. P. 1934 *Cold Spr. Harb. Symp. Quant. Biol.* **2**, 181.

Winsor, C. P. 1937 *Quart. Rev. Biol.* **12**, 348.

Yule, U. G. 1925 *J. R. Statist. Soc.* **88**, 1.