



Interspecific Competition

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INTERSPECIFIC COMPETITION

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(With 3 Figures in the Text)

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I. INTRODUCTION

The section of Darwin's theory of natural selection concerned with the struggles for existence, as developed in the third and fourth chapters of *The Origin of Species*, contains the following argument: (1) The potential rate of increase of organisms is greater than that which the resources of the environment can support. (2) The range of physical conditions in which a given organism can survive, and the kind of matter which it can convert into the tissues of its own species (i.e. the range of conditions to which it is adapted) are limited. (3) The failure of organisms to survive or to be born may then be due to any of three agencies: (a) the direct action of the physical environment, e.g. climate or soil; (b) other organisms apart from competitors (predators, parasites, etc.); or (c) competition, defined as the demand, typically at the same time, of more than one organism for the same resources of the environment in excess of immediate supply (Darwin, 1859, pp. 62-3; cf. Clements & Shelford, 1939,

pp. 159-60). The proportion of organisms eliminated by competition decreases with the increasing severity of the physical environment, predation, or any other agency reducing the ratio of population to resources. (4) When competition occurs it is severest between organisms with the most similar needs and habits. (5) In general, similarity in needs and habits tends to be greater the closer the taxonomic relationship. Hence (6) as new forms appear in a given locality, either by evolving there or by migration after divergence elsewhere, they will either eliminate or be eliminated by their nearest relatives if they compete with them, unless (7) each form becomes adapted to its own special habitat, when competition between them ceases in those habitats and all may survive together.

It is proposed to consider Darwin's thesis by examining, first, examples of competition between different species and varieties under both experimental and natural conditions, and secondly, differences in ecology (structure, habit) or distribution which may be attributed to competition. In most of

the examples the competing forms will not interbreed. Such breeding barriers may arise through genetic changes (e.g. polyploidy) within an interfertile group, but more often they appear to have arisen after some form of geographical or ecological isolation. The principles are exactly similar if two competing forms, e.g. mutant and wild type, do interbreed. In each case genes producing certain phenotypes are eliminated by differential survival: the study of this, as Robson & Richards (1936) emphasize, is essential to the demonstration of selection in natural populations. Interbreeding merely complicates the situation: the mutant gene is potentially able to spread through whole population and may, for instance, escape elimination by becoming recessive (see Fisher, 1930; Dobzhansky, 1941; Huxley, 1942; Mayr, 1942; and Mather 1943).

(a) Factors governing population growth in general

All organisms tend towards unlimited increase, but in this they meet resistance from their physical and biological environment (Chapman, 1931). There are thus three factors involved: (a) the organism itself, i.e. the range of environmental conditions to which it is adapted and characteristics such as its life-history and method of reproduction, (b) the physical or abiotic environment, e.g. climate and soil, and (c) the biological environment, comprising the effects of organism upon organism, which occur either directly, or indirectly through the reaction of organisms upon the physical environment, e.g. 'conditioning' of the medium by waste products and consuming food. The operation of biotic factors is usually density-dependent and that of abiotic factors independent of population density (Smith, 1935; Thompson, 1939). These factors may in turn stimulate, inhibit or be neutral towards the increase in density or distribution of the whole community of organisms or of certain species within it (Clements & Shelford, 1939).

Changes in population density are determined by the rates at which adults are produced and die. Such changes, i.e. the rate of population growth, are the measure of success in the struggle for existence, of which competition is a part. In organisms reproducing sexually with cross-fertilization, the upper limit of the rate of production of adults for the whole population is set by the average rate of production of male and female gametes and the sex-ratio. With self-fertilizing hermaphrodite organisms this upper limit is set simply by the rate of production of gametes, and with organisms reproducing asexually by the rate of division, budding, spore-formation, parthenogenesis, etc. Failure to reach this upper limit may be due to causes operating at any stage of the life-history. These causes fall into the three cate-

gories distinguished above. According to Clements & Shelford (1939, p. 180), who give an historical summary and an extensive review of the literature, 'there are eight causes of failure to produce a large number of later juvenile or adult offspring.... They are (1) decrease in the number of eggs produced or fertilized, owing to various causes, or destruction of eggs and very young stages; (2) death of adults and late juvenile stages from adverse physical conditions; (3) destruction by enemies and disease; (4) quantitative or qualitative insufficiency of food; (5) unsuccessful competition for space, shelter or food; (6) physiological changes in reproductive vigor; (7) initial shortage in reproducing population; (8) cannibalism. To these one may add certain assumptions such as loss of immunity, etc. but of these little is definitely known'.

The operation of the three types of causes and the relation between them have recently been discussed by a number of authors, to whose writings a general guide may usefully be given at this point. The subject has been discussed in general by Elton (1927, 1930, 1933), Chapman (1931), Prenant (1934), Bodenheimer (1938), Clements & Shelford (1939), Pearse (1939) and Severtzoff (1941); while Pearl (1925), Allee (1927, 1931, 1934), Gause (1934), Hammond (1938, 1939), Park (1938), Vevers (1938, 1939), MacLagan (1941) and D'Ancona (1942) have reviewed the literature on the operation of density-dependent factors.

Work analysing the determinants of population growth of particular organisms or from a particular point of view is reviewed by the authors given in the list which follows. Reference to further original papers is made in the 'Notices of publications on the animal ecology of the British Isles' in the *Journal of Animal Ecology*; in the reviews of ecological literature in the *Journal of Ecology*; and in the 'Current Bibliography' of the *Journal du Conseil Permanent Internationale pour l'Exploration de la Mer*; other original work is discussed in § 1(a) of the present paper.

Bacteria: Buchanan & Fulmer (1928-30) and Hinshelwood (1944) on populations of bacteria and other microorganisms in the soil, Zobell (1946) on marine bacteria.

Yeast: Richards (1934) on yeast growth (with mathematical treatment), Williams (1941) on growth-promoting nutrilites for yeasts.

Fungi: Garrett (1934, 1938, 1939, 1944) on soil-borne fungi, particularly in relation to root disease.

Other plants: Clements (1916), Clements, Weaver & Hanson (1929) and Tansley (1939) on plants in general, particularly in relation to ecological succession.

Protozoa: Jahn (1934), Johnson (1937, 1941), Allee (1941), Hall (1941a), and Richards (1941) on

the growth of protozoan populations with particular reference to density-dependent factors, Taliaferro (1941) on blood-dwelling species, Hall (1941b) on food requirements; Hall & Shottenfeld (1941) on density and population growth of *Glaucoma pififormis*.

Rotifera: Edmondson (1944, 1945).

Crustacea: Gause (1932) on population growth, Berg (1934) and Banta (1937) on population density and sex-determination in Cladocera; Wilder (1940) on density and population growth of the amphipod *Hyalella azteca*.

Insects: General. Chapman (1939), Imms (1937) and Voûte (1943) on population growth in general, Uvarov (1931) and Gause (1932) on the influence of the physical environment, Graham (1939) on forest insects, King (1939) on soil insects, Carpenter (1940) on insect outbreaks.

Parasites, fluctuations and biological control: Smith (1939), Thompson (1939) and Clausen (1940) on the subject in general, Nicholson & Bailey (1935) and Smith (1935) on mathematical treatment, Flanders (1939, 1942) on the control of the sex-ratio and of oviposition, respectively.

Social insects: Bodenheimer (1937a, b), Emerson (1939a, b).

Experimental populations: Ford (1937), Park (1937, 1941, 1942), Crombie (1944a, 1945, 1946); Robertson & Sang (1944a, b) on population growth of *Drosophila*.

Marine life: Lucas (1938) on plankton, Harvey (1942) on the production of plant life in the sea, Russell (1942) on fish, Burkenroad (1946) on starfish, Zobell (1946) on marine bacteria.

Mammals and Birds: Severtzoff (1934, 1941) and Elton (1930, 1942) on population growth, Kendeigh (1944) on the measurement of bird populations, Hammond (1941) on fertility.

Man: Carr-Saunders (1922) and Hogben (1931) on the biological aspects, Carr-Saunders (1936) and W. S. Thompson (1942) on the social aspects, and Kuczynski (1935) on the measurement of population growth. On the history of human population theory: Malthus (1798), Strangeland (1904), Bonar (1931).

Comparative mortality: Pearl (1922), Pearl & Miner (1935), Davis (1945).

Outbreaks and sunspot cycles: Clements & Shelford (1939), MacLagan (1941).

Fluctuations of predator and prey, and epidemics: Gause (1934, 1935), Volterra & D'Ancona (1935), D'Ancona (1942); Topley (1926, 1942) and Greenwood *et al.* (1936) on experimental epidemics.

Mathematical treatment of population growth and competition: Lotka (1925, 1934, 1939, 1945), Gray (1929), Gause (1934, 1935), Volterra & D'Ancona (1935), Kostitzin (1937), D'Ancona (1942), D'Arcy W. Thompson (1942); other references in

Crombie (1945, 1946); Leslie (1945) on the use of matrices.

(b) Factors tending to reduce competition

Only density-dependent factors are directly involved in competition although density-independent factors may, through the competing organism's intrinsic nature (e.g. adaptation to different environmental conditions), determine the outcome of competition and also whether it occurs at all. Competition is reduced by factors which keep the ratio of population to environmental resources low and increased by those which produce the reverse effect. Such factors may be classified under three headings.

(1) The organism itself

(a) The mortality which occurs at different stages of the life-history as a result of competition will vary from organism to organism according to its method of reproduction. If the adults continue to reproduce regardless of the resources available, competition will occur and supernumerary individuals be eliminated in either the juvenile or adult stages. If the adults limit their rate of reproduction, e.g. by less frequent union between the sexes, special control exerted by the female over her rate of oviposition, or by the control of the number of reproductive individuals such as occurs in ants, bees or termites, mortality will be reduced. Elton (1927, pp. 123-5) points out that animals near the predator end of food-chains tend to have special means of regulating their numbers, e.g. by a very low rate of reproduction or the habit of having nesting territories. According to Lack (1946), bird predators of the lemming and other rodents have, besides emigration, another uncommon adaptation to the huge fluctuations of their prey. When prey is very abundant they often raise two broods a year instead of one and have clutches of up to double the size, while when their prey is very scarce they do not attempt to breed.

Control of the reproductive rate may be a response to population density. When the rate of oviposition or birth of young is regulated by competition for space among adult animals the ratio of offspring to food supply will be lower and so a higher proportion of those born will survive. Lack (1943, ch. 8) considers that the territorial behaviour of birds is unlikely to limit population in this way, but the question is one which should be examined with reference not only to birds but to other animals which possess territories (cf. Bodenheimer, 1938; Clements & Shelford, 1939; Dobzhansky, 1941, p. 170; Elson, 1942). Competition for space which limits population, although relatively unimportant compared with other factors, occurs in insects which compete for definite oviposition sites, e.g. the weevil *Sitophilus oryzae* (MacLagan, 1932; MacLagan & Dunn,

1935), the beetle *Rhizopertha dominica* and other insects (Crombie, 1942, 1943). Competition for mates which reduces the frequency of mating would have the same effect (cf. MacLagan & Dunn, 1935; Reynolds, 1944; Flanders, 1945).

References to control of oviposition depending on the presence and quantity of suitable larval food and sites for development are given by Russell (1941). Striking examples of this are to be found among entomophagous insect parasites in which, like many other Endopterygota, adults and young occupy different environments (Clausen, 1940). The adult female must first be able to find the hosts on which her larvae feed. The rate at which this occurs is determined not only by host density, but by the skill shown by the parasite in her search (cf. Thorpe & Caudle, 1938; Laing, 1937, 1938; Varley, 1941; Wilkes, 1942). As de Bach & Smith (1941a) point out, such skill is a specific characteristic. The rate of oviposition depends upon this and two other processes: oogenesis whereby eggs are produced, and oviposition whereby, in response to a group of stimuli which would be normally obtained only from the appropriate host, eggs are laid. According to Flanders (1942), in some Parasitic Hymenoptera, oogenesis does not occur unless the female is able to feed on the host appropriate to its larvae. When conditions are favourable to oviposition, the number of eggs which each species places on each individual host is fairly constant and largely independent of host density. This is achieved on the one hand by the females having a ready supply of eggs available when hosts are found, and on the other, when suitable hosts are few, by their ability both to discriminate between parasitized and unparasitized specimens and to exercise restraint from oviposition in the former (cf. Salt, 1934, 1937; Ulliyett, 1936; Jacobi, 1939; Lloyd, 1939, 1940). By such restraint they are able to prevent mortality in the immature stages through overcrowding. The maintenance of reproductive capacity when environmental conditions are unsuitable for oviposition, and the ability to restrain from oviposition, which is essential to host selection, are made possible by two adaptations. Some species store ripe eggs. Others have eggs which cannot be stored longer than the incubation period. In them oösorption sets in and proceeds at the same rate as oogenesis until conditions suitable for oviposition once more arise.

(b) Changes in the organism itself may occur which alter the existing relationship between biotic potential and environmental resistance or cause organisms of different species to cease to interfere with each other and so affect competition. Some changes of this kind are at present not always referable to causes outside the organism itself, e.g. genetic mutations and changes in physiological vigour, such as the

changes in reproductive rate and viability of insects and other animals and in the resistance of the host-plant or animal noted by Clements & Shelford (1939), Carpenter (1940) and Shelford & Flint (1943). Others are known to be responses to the environment, but are independent of population density, e.g. changes in response in given aspects of the environment such as those brought about by 'olfactory conditioning' in insects (Thorpe, 1930, 1940; Crombie, 1944b) and other forms of learning (Thorpe, 1943a, b, 1944a, b) which may enable an animal to make use of a new food or habitat. Others are brought about by competition itself, e.g. changes in size, sex-ratio, reproduction, rate of development and longevity, and changes in morphology and behaviour as in aphids and locusts (Allee, 1931, 1934; Hammond, 1938, 1939) and in the insect parasites described by Salt (1941). An example of dwarfing due to crowding in plants is described by Mason (1915) in his work on the lodgepole pine. Two important examples of changes of this kind are the 'adaptation' undergone by plants (§2(b)) and the observation by Shelford (1911), in his study of ecological succession in fish, that the succession of species is the result of the stability of the *mores* (physiology, behaviour, habits and mode of life). When *mores* are flexible, species do not succeed one another when changes occur in the environment, but the same species remain there with changes in behaviour and physiological characters.

(2) *The physical environment*

This may reduce competition in two ways: (a) It may cause an increase in food or other resources fast enough to allow a rapid increase in populations of the competitors. Elton (1930), Clements & Shelford (1939) and Timoféeff-Ressovsky (1940) have drawn attention to the importance of this and it is sufficiently obvious in the dependence of many population changes upon climate and weather (e.g. Rivnay, 1938; Andrewartha, 1944; and Ribbands, 1944 on insects; Cross, 1940 on mammals). But environmental resources cannot go on increasing for ever and a time must come when competition will occur, unless prevented by something else. (b) It may adversely affect the competitors, but not their food, living space, etc., so that the ratio of population to resources remains low. This occurs in unfavourable habitats such as deserts and high mountains where among plants there are 'open communities' (Tansley, 1939), and may also affect lichens on rocks and the inhabitants of swiftly moving streams. As Darwin points out: 'On the confines of its geographical range, a change of constitution with respect to climate would clearly be an advantage to our plant; but we have reason to believe that only a few plants or animals range so far, that they are destroyed

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by the rigour of the climate alone. Not until we reach the extreme confines of life, in the Arctic regions or on the borders of an utter desert, will competition cease' (1859, p. 78). It is there too that the most violent fluctuations in numbers and also migratory movements are likely to occur (Huntington, 1931; Carpenter, 1940). Under exceptional circumstances a density-independent physical factor may allow organisms exactly to replace themselves from generation to generation. But except for this very improbable case, if the organisms survive at all in its presence, such a factor could not itself limit population growth and suspend competition more than temporarily. Either the organisms will not be viable in its presence, or if they are they will increase until they compete for something, e.g. if not for food then for space—as in swiftly running streams where there may be competition for lodging sites, and this will limit population density.

(3) The biological environment

One organism may reduce the competition occurring between members of another species (or between two other different species) in a number of different ways: (a) Being the food of the latter it may increase rapidly. In a finite world the increase of the food will eventually reach a limit, but while its rate of increase is greater than that of the organisms feeding on it, i.e. while 'temporarily super-abundant' (Lack, 1946), there will be no competition between the latter. A situation in which competition is temporarily reduced, if not prevented, is exemplified by the changes in populations of predators or parasites which follow those of their prey or hosts, e.g. Cutler & Crump (1920) and Cutler, Crump & Sandon (1922) on fluctuations of soil bacteria and Protozoa; de Bach & Smith (1941b) on fluctuations of insect hosts and parasites; Huntsman (1941) on fish and birds; and Crombie (1944c) on rats and cats. (b) It may prey on or parasitize the competitors. In his discussion of optimum population density Elton (1930) points out that without predators to control its numbers an organism is in danger of increasing above the population the food supply can support. This seems to have happened to the Kaibab deer (Rasmussen, 1941). Fuller (1934) points out that competition among fly larvae attacking carcasses is relieved by the parasitism of Hymenoptera (cf. Brues, 1923). Similar examples are given by Severtzoff (1934), Clements & Shelford (1939) and Errington (1946). But agencies such as predators may produce a different kind of competition rather than preventing it altogether. They may, for instance, prevent competition for food among their hosts, but cause them to compete to avoid the predators, e.g. there may be selection for reflexes which assist

this. (c) An organism may suppress all the competitors by more powerful competition for the resources for which they compete, perhaps leaving them to survive in separate niches for which they do not compete with each other. (d) It may react upon the environment so as to affect the conditions of competition. The third and fourth effects are brought about especially by ecological dominants which may reduce competition among subordinate forms. There is probably little intraspecific competition among the subordinate insects in the sewage beds described in § 2(e) or among the less successful species of granivorous insects of which a small population manages to survive in special niches in a medium dominated by its more powerful competitor. A similar effect upon subordinates may be brought about by reaction upon the environment. This is more characteristic of some plant dominants (§ 2(b)). An example from animals is given by Cahn (1929), who claimed that carp introduced into a lake transformed the bottom vegetation and other aspects of the environment so that the other species of fish were reduced to very small numbers.

(c) Consequences of interspecific competition

Competition occurs between species with similar needs and habits when the ratio of their population to environmental resources reaches a certain value. This ratio may be kept low and competition prevented by the various agencies discussed above. When competition does occur external factors may change at intervals (e.g. seasonally), alternately favouring one then the other of two competitors, so that first one tends to increase at the expense of the other and then the latter at the expense of the first. Such a situation would produce forced fluctuations in populations of the two species. But if external conditions (other than those brought about by the organisms themselves, for these are part of the process of competition) remain constant enough not to reverse their competitive relationship in this way, it may be demonstrated by a simple argument that two species with *identical* needs and habits cannot survive in the same place if they compete for limited resources—at least not if their needs and habits remain identical. The same conclusion applies to organisms with *similar* rather than identical ecology, but the necessary degree of similarity can only be discovered empirically. This conclusion is explicit in *The Origin of Species* (Darwin, 1859, pp. 75, 110–15) and the biological consequences of this situation have recently been developed by Gause (1934) (see also Lotka, 1925; Volterra, 1926; Kostitzin, 1937; Volterra & D'Ancona, 1935; D'Ancona, 1942).

Now the superiority of one species over another must be estimated in terms of the whole life-cycle,

and must include adaptability as well as adaptation (§2(c)). Individuals of one species may then be superior to those of another in two different ways: (a) in the combined *rate of reproduction and survival* independent of interspecific interference: this will depend on adaptation to the environment, or (b) in *interference* (through direct attacks, conditioning the medium, consuming food, etc.) which reduces the rate of reproduction and survival of the competitor. A superior rate of reproduction and survival of course affects the competing species through interference: if there were no interference, there would be no competition. But the two modes of superiority are distinct (de Candolle, 1820; Lyell, 1830–33; Darwin, 1859, p. 69).

Let x and y be two species with identical needs and habits competing for the same resources of a limited environment. There are two cases:

(1) Suppose x to be superior to y in interference, but equal in rate of reproduction and survival. Then if at some time the two species have equal populations, each will reduce the succeeding generation of the other, but x will reduce y 's proportionately more than y reduces x 's. The advantage of x over y is a property of each individual, so that the total advantage of the population of x over that of y will depend on the number of individuals of each species present. x will then form more and y less than half the total population, and its relative advantage over y will therefore have increased. This will lead to a still greater relative increase of x in the second generation, which, in turn, will give it an even greater relative advantage over y , and so on, since there is nothing to make y approach a limit other than zero, until the latter is entirely eliminated from the ecological niches for which it competes with x . It may of course survive in niches in which it is superior to or does not compete with x . If y began with a sufficient numerical superiority, the advantage would then go to this species and it would eliminate x , the critical numerical superiority required depending on the 'amount of advantage' of an individual x over an individual y and on the exact conditions of the struggle.

(2) Now let the interference of each species with the reproduction and survival of the other be equal, and let x have a higher rate of reproduction and survival than y . The total number of individuals which a limited environment can support is limited. Let the number of x and y be equal at some time when the total population is approaching its limit. Owing to lack of food, space, etc. in the first generation after that, each species will lose a proportion of its numbers, the proportions being equal since the interference of each species with the other is equal. But as x increases faster than y it will now represent more than half the total population. In the second generation the proportions of their numbers lost by

the two species will again be equal, but the absolute numbers of x will again be relatively greater; and so on until x alone remains. As before, if y began with a sufficient numerical superiority, the critical value of which depends on the relative rates of reproduction and survival of the two species, it would in the same way be able to eliminate x .

It is conceivable that the advantages of two species derived from the rate of reproduction and survival, interference and numbers may at some time be precisely balanced. But since the balance would depend on numbers as well as on the other factors, and since in nature numbers are subject to fluctuations caused by environmental changes, such a balance would be highly unstable. It follows, then, that if the conditions enumerated above which allow competition are fulfilled, two species with identical needs and habits will not survive together in the same limited environment. By a similar argument Nicholson & Bailey (1935, p. 582) have shown that when two or more host-species are attacked by a common parasite-species only one host is likely to survive. A corollary to this theoretical conclusion, which seems inescapable, is that if in nature such species are found together, then either one or more of the necessary conditions must be lacking, or the species must differ in their ecology.

One special point seems worth mentioning here. If two competing species meet along an environmental gradient each end of which favours one of them, there would theoretically be a certain point on the gradient on either side of which each would be superior to the other (cf. Gause & Witt, 1935). Each would then exclude the other from its favoured area and the boundary between them would be sharp. Examples of this situation are given in §2 (e.g. Beauchamp & Ulyott, 1932; Gause, 1936). But in nature where environmental conditions fluctuate this boundary would be continually moving, describing an area in which the two species would be in a state of unstable overlap (Lack, 1945). Finally, while the argument applies to monophagous and polyphagous species with the same food and habits, Lack (1946) has drawn attention to the complexity of competition between polyphagous species with slightly different food preferences and the importance of the time factor. For instance, two species which compete for common food most of the time may survive together because of the occurrence, at intervals shorter than the time it takes for one species to eliminate the other, of periods of temporary abundance of a second food to which one of the competitors transfers its complete attention, during which periods each species is able to re-establish its numbers without interference from the other. Such examples serve to remind us of the complexity of the interrelationships between organisms in nature.

2. INTERSPECIFIC COMPETITION IN EXPERIMENTAL CULTURES AND IN THE FIELD

The factors controlling population growth and the ecological relations between competing species have been accurately determined in only a limited number of cases. Only when this has been done can the operation of the theoretical conclusions reached in §1 be examined. But for the assistance of others proposing to study this subject reference will be made below to all the important work known to the author dealing with interspecific competition. Only a very summary analysis has been made of non-zoological literature.

(a) Plant microorganisms

Interactions between plant microorganisms in general have been reviewed by Fawcett (1931), Nicol (1934), Russell (1937), Waksman (1937) and Garrard & Lockhead (1938); while Holman (1928) and Buchanan & Fulmer (1930) have paid particular attention to bacteria in their hosts and in artificial media (cf. Régnier & Lambin, 1934). White, Robinson & Barnes (1938) describe 'transformations' in pneumococci which may involve selection between different biotypes. Garret (1934, 1938, 1939), Porter & Carter (1938), Weindling (1938) and D'Aeth (1939) review interactions between fungi in the soil, the host plant and in artificial media (cf. Lal, 1939).

Many types of interaction occur between plant microorganisms, from reciprocal symbiosis or stimulation of reproduction to antagonism involving inhibition or destruction. There are three main explanations of these phenomena: competition for energy materials and nutrients or synergetic effects in which the metabolic products of one organism form a suitable source of energy and food for the other; changes in the environmental conditions of the substrate, e.g. in pH or oxidation-reduction potential, brought about by one of the organisms; and the formation of specific substances (enzymes, toxins, stimulants) which directly affect the other organism. Among soil fungi some saprophytes actually attack and assimilate the mycelium, etc. of other parasitic forms (Garrett, 1939). These complicated interactions lead to a state of mutual equilibrium between the populations of microorganisms in the soil. The modification of this, e.g. by the increase of one group of organisms, leads to the depression of others, e.g. near competitors. Environmental conditions, e.g. temperature, pH, moisture, aeration and the presence of specific nutrients, often have a selective effect enabling the organism which they suit best to develop more rapidly and suppress the others. Environmental conditions may affect the production of toxins as well

as the growth of an organism and competition for the same food supply.

Among fungi, according to D'Aeth (1939), two organisms may grow together in the same place in the host plant and develop independently as long as their spheres of physiological activity do not overlap. Nicol & Thornton (1941) worked on competition between related strains of nodule bacteria and its influence on infection of the legume host. When two strains are both present in the surroundings of their host root system, active competition between them may cause the strain having the higher initial growth-rate almost completely to check the multiplication of the other strain outside the plant. This dominant strain will then be responsible for nearly all the nodules. 'This competition can be compared with the intraspecific selection that takes place in higher organisms and may well be more acute than competition between more distantly related micro-organisms whose environmental requirements are more dissimilar.'

Gause (1934) studied the competition in an artificial media between two yeasts belonging to different genera. Beginning with small inocula the growth of each was inhibited under aerobic conditions by the ethyl alcohol produced, and under anaerobic conditions by this and probably other metabolic waste products. Growth ceased before the food supply was exhausted and both kinds still existed together when the experiment ceased. As the exact chemical constitution of the media is unknown it is impossible to say to what extent they competed for the same nutrients, although Gause (1935, Table 2) seems to assume that one would have eliminated the other (the victor depending on the conditions) had the experiment continued.

(b) Higher plants

The large literature on competition in plants has been reviewed by Warming & Vähä (1909), Clements (1916), Clements, Weaver & Hanson (1929), Salisbury (1929, 1940) and Braun-Blanquet (1932), while additional work is discussed by Gause (1934, 1936), Cain (1939), Carpenter (1939), Clements & Shelford (1939), Tansley (1939), Diver (1940), Dobzhansky (1941), and Huxley (1942). Stapledon & Davies (1928) and Davies (1928) describe competition between species in seed mixtures; Bystríkov (1931) competition between various cultivated plants; Eisele & Aikman (1933) competition in pastures; and Pavlychenko & Harrington (1934) the competitive efficiency of weeds and cereal crops. Only the briefest statement of general conclusions will be given here.

According to Clements, Weaver & Hanson (1929, pp. 316 et seq.), who give a complete survey of the field and an account of their own extensive experiments: 'Competition is purely a physical process.

With few exceptions, such as the crowding up of tuberous plants when grown too closely, an actual struggle between competing plants never occurs. Competition arises from the reaction of one plant upon the physical factors about it and the effect of these modified factors upon its competitors. In the exact sense, two plants, no matter how close, do not compete with each other as long as the water-content, the nutrient material, the light and heat are in excess of the needs of both. When the immediate supply of a single necessary factor falls below the combined demands of the plants, competition begins.' 'As a figure of speed, competition for space is probably not objectionable, but it must not be overlooked that space really stands for the raw materials, energy and working factors that it contains.' 'Water stands first, light next, and nutrients last in native communities, with the order of light and nutrients reversed in the case of many intensive field crops. The general and probably universal rule is that the factor present in the smallest amount relative to the demand will be paramount' (see Rübel, 1935). The relations between all parts and processes of different plants may affect the competition between them. Competition seems to be constant between certain members of a closed plant community, both between individuals of the same and those of different species. In seral communities new plants are always entering and competing with those already there, and this leads to the succession characteristic of such communities. The final result is the dominance of species (usually the tallest) with the controlling reaction on water, light or nutrients and subordination of the rest. The number of dominant species is usually small, occasionally only one, even in such communities as West African tropical forests where the diversity and number of species in the community is great (Aubréville, 1938, pp. 125 et seq.), but this is unusual among tropical forests as a class. As dominance increases and unsuccessful species are eliminated competition decreases, e.g. in a climax forest there is probably little competition between the trees and the ground layer of herbs. But even in climax communities, owing to the seasonal production of new shoots and seedlings and the continuous variation of physical factors, competition still occurs, e.g. between the associated individuals of both dominant and subordinate species and between adults of the latter and seedlings of the former. Such competition 'serves to keep the composition of the population and the structure of the community substantially constant, the various classes of members being in approximate equilibrium with one another, and the community as a whole with its habitat. Thus competition between the members for light or for water maintains the community in a stable condition, preventing any one species from breaking away from

its existing status in the community—as it may do if other members of the community are removed—and fresh species do not normally enter a climax community' (Tansley, 1939, p. 227).

According to Clements, Weaver & Hanson (1929), competition within a single species is keenest when individuals are most similar. With plants of different species the closeness of competition varies directly as their likeness in vegetation or habitat form, and is independent of their phylogenetic relationship except in so far as this is based upon life-form or habitat-form. This principle is of primary importance in the competition that arises between occupants and invaders in the different stages of ecological succession. A plant similar to those in a community is excluded, but 'the species so unlike the occupants that they enter at a clear advantage or disadvantage, establish themselves readily, in one case as a result of the reaction, in the other by taking a subordinate position' (Clements, Weaver & Hanson, 1929, p. 21). Competition may be avoided by separation in time (season of growth or reproduction) as well as space (height, position of shoot and root). Subordinate species in a community survive when they differ sufficiently from others or when they undergo adaptation, i.e. the adjustment of functions with consequent modifications of structure and form in response to physical factors modified by the reaction of competitors. Such functional changes involve 'absorption and root pressure, conduction, stomatal movement, transpiration and starch-content, as well as other features such as turgidity, osmotic concentration etc.' (Clements, Weaver & Hanson, 1929, p. 322). The extinction of one most often occurs when two species are similar in life-form, especially when one enjoys a marked advantage in the reaction upon light or water-content. The species which arrives first is often able by its numbers of well-rooted and reproducing individuals to suppress new-comers. Other points favouring success are duration and perennation, rate of growth (root and shoot), rate and amount of germination and vigour and hardiness especially under adverse conditions. Occasionally one species suppresses another by toxic products: thus the refuse of bracken (*Pteridium*) is injurious to some of its competitors and prevents their growth (Jeffreys, 1917; Farrow, 1925). Sometimes competition keeps plants within a narrower ecological range than they can tolerate (Salisbury, 1929). For instance, many maritime plants grow as luxuriantly or even more luxuriantly in garden soil than in their natural habitats, and their absence inland is presumably to be attributed to intolerance of competition. With pairs of calciphile and calciphobe species or different ecotypes (Tansley, 1917; Stapledon, 1928; Turrill, 1931, 1940), each is successful in its own habitat and is suppressed in and eventually eliminated from that

of the other. According to Braun-Blanquet (1932, pp. 15–16), however, the role of competition has here been frequently over-emphasized, since in many cases the basiphilous species could not survive in the habitat of the acidiphilous species and vice versa, even without competition. Sometimes the success or failure of competing species is influenced by their susceptibility to factors such as animal grazing. This is illustrated by the effect of rabbits on the vegetation of the Breckland (Farrow, 1925).

Competition is severest and 'as the final term of suppression (extinction), is most in evidence between similar life-forms' (Clements, Weaver & Hanson, 1929, p. 321). In many of the experiments described by these authors, competition between two species with similar ecology resulted in the elimination of one of them, and the results suggest that had they been continued long enough the same would have occurred in all of them. But such puzzling cases as that described by Diver (1940) are common in botanical observation. The two species of rush, *Juncus conglomeratus* and *J. effusus*, are so closely related that they were formerly regarded as two forms of one species *J. communis*. The differences between these are apparently small although definite, but the former has the narrower range of tolerance and rarely occurs alone. Where they occur together, 'so closely may they intermingle that on one occasion it was necessary to dig up a tuft to demonstrate (to a botanist) that the two species were not growing from the same root stock'. It is true that sessile habit and long life may defer the outcome of competition in plants so that observations over many years may be necessary to decide whether one species will be eliminated. But it is clear that the theoretical problem raised in § 1 suggests the need for intensive ecological studies from this point of view.

(c) Protozoa

(1) *Cultures*. Gause (1934, 1935) describes experiments carried out to study the competition between two or more species of Protozoa living on the same food. In some cases they occupied the same ecological niche and in others different ecological niches. Summaries of this work are given by Gause (1937) and Richards (1941).

Paramoecium caudatum and *Stylonychia mytilus* were grown separately and in mixed cultures in an oatmeal infusion inoculated with *Bacillus subtilis*. Each species depressed the population growth of the other as compared with growth in pure cultures, but *Stylonychia mytilus* depressed *Paramoecium caudatum* very much more than the latter did the former. With a denser oatmeal infusion sown with various wild bacteria the positions of the two species were reversed. *P. caudatum* reached the same population as when living alone. *Stylonychia mytilus* reached

about half this value and then declined, but was not eliminated completely. As the exact conditions in the medium are unknown it is impossible to tell for what parts of the environment competition occurred.

When competing in a regularly renewed (unconditioned) medium containing *Bacillus pyocyanus* as food, *Paramoecium aurelia* has two advantages over *P. caudatum*: the rate of geometric increase of the biomass of the former species is higher (1.1244 as compared with 0.794) and it accumulates a greater biomass (1.64 times) than *P. caudatum* at the expense of the same amount of food. In mixed cultures the two species increased unaffected by the presence of the other for the first few days, until the population had reached the maximum which the limited but constant amount of food could support. Up to this time each species was seizing the still unused resources of energy. Thereafter *P. aurelia* increased to the same population as when living alone and *P. caudatum* decreased to zero population. During this period there was a redistribution of completely seized energy between the two species. The reason for the lower rate of increase of *P. caudatum* in this medium is that it is more sensitive than *P. aurelia* to the waste products of the pathogenic bacterium *Bacillus pyocyanus*. With yeast and a less virulent strain of this bacterium as food, *Paramoecium caudatum* had the higher rate of geometric increase of the two species and was more successful in competition. *P. caudatum* is also more sensitive than its rival to their own waste products. When the medium (without the virulent bacterium) containing the mixed culture was unrenewed, the initial rate of increase of *P. caudatum* was higher, but *P. aurelia* lived twice as long on the limited food present. With yeast as food *P. aurelia* had a lower rate of geometric increase than *Glaucoma scintillans* ($b=4.625$) and was driven out by it. In mixed populations of either *Paramoecium aurelia* or *P. caudatum* with *Stylonychia pustulata* (with *Bacillus pyocyanus* as food) the latter protozoan was always driven out, apparently because of its sensitivity to the waste products of the bacteria.

In a renewed medium containing yeast as food *Paramoecium aurelia* and *P. bursaria* were able to survive together in a mixed culture because the former feeds in the suspension in the upper layers of liquid while the latter feeds on the bottom. The populations of the two species reached the same position of equilibrium irrespective of initial concentrations except when the initial superiority of *P. bursaria* over *P. aurelia* surpassed a certain limit. *P. caudatum* and *P. bursaria* were also able to survive in a mixed culture in a renewed medium containing both yeast and bacteria as food, because the latter feeds on the yeast on the bottom and the former on the bacteria suspended in the upper layers of liquid (cf. Singh, 1942). Again the same equilibrium position

was reached regardless of initial concentrations except when *P. caudatum* began with too great an initial inferiority, when its sensitivity to the waste products of *P. bursaria* prevented its further increase. In these experiments under controlled conditions it proved true that two competing species cannot survive together in the same place if they have the same needs and habits, i.e. occupy the same ecological niche. Gause (1934, 1935) found that the Lotka-Volterra equations gave at least a qualitative description of the changes in biomass of the two species. These equations will be discussed in a later section. Gause & Witt (1935) adapted the equations to cover the case of the 'special zone' described above where the equilibrium position was not returned to when one species began with too great an inferiority. This is of obvious importance in nature, e.g. in the establishment of plants.

Gause (1936) describes an experiment designed to study the effect of a gradual change in an external physical factor (*pH*) on the competition between two species. Above a certain value of *pH* one was successful and below this the other. The change in population at different *pH* values was sometimes physiological and independent of competition, and sometimes entirely due to the competition of a rival better adapted to the particular *pH* value. The mathematics of such a change in competitive ability in response to a gradual environmental change are discussed by Gause & Witt (1935). In an article on the relation of phenotypic adaptability to genotypic adaptation Gause (1942) describes competition, in cultures of *Paramoecium* of various species, between clones of two mating types (between which there is no conjugation). In the case of adaptation of *P. caudatum* and of *P. aurelia* to the increasing salinity of the medium, the larger part of the total adaptation is due to adaptability. The clones that survived in mixed cultures are here weak in initial strength but powerfully adaptable. On the other hand, in the case of acclimatization of *P. caudatum* to dilute solutions of quinine, adaptability is low as compared with the inherent diversity of various clones in initial resistance. The survivors here are well adapted but poorly adaptable. The different clones of the same species occupied identical niches in which only one was able to survive.

(2) *Field observations.* Interspecific competition enters into the process of succession of Protozoa in natural populations. Woodruff (1912, 1914) believed that in hay infusions the sequence of dominant species is determined by the rate of increase and the effect of specific excretory products. Gause (1936), in a review of the 'principles of biocoenology', describes the formation of protozoan climaxes in glass plates submerged in natural waters. There is an initial period when all the chief components of the

community increase, followed by a period of reconstruction when competition eliminates some of the species and leaves a stable population of dominants occupying the principal ecological niches. In nature, according to Hutchinson (1941), the primary requirements of non-flagellate groups of Protozoa are light, heat and nutrient elements. The autotrophic forms live under conditions of competition for nutrient substances. Very few divisions are needed to raise a species to a dominant position. Different minimal concentrations of different elements required for the maximum division rate would probably be found in different species. This provides a mechanism for succession during the period of nutrient exhaustion after a maximum for any species, for as the concentration falls the species responsible for the depletion, which dominates the initial nutrient level, will suffer from competition from other forms which are dominant at low nutrient levels. Interactions between Protozoa and other organisms in the soil are mentioned by Russell (1937) and Waksman (1937).

(d) *Invertebrates other than Protozoa and insects.*

Beauchamp & Ullyott (1932) studied competition between different species of freshwater triclad flatworms (Platyhelminthes) in mountain streams, and found that mutual competition restricts certain species to a narrower habitat than that in which each is capable of living when competitors are absent. When *Planaria montenegrina* and *P. gonocephala* occur in competition with each other, temperature is the factor which governs their relative success, the former dominating in parts of the stream of which the temperature is below 13–14° C. and the latter in (lower) regions where the temperature is above this value. This is an example of a gradually changing physical factor causing a sudden change in competition relations between two species and the equilibrium position reached by their populations. When *Planaria alpina* competes with *Polycelis cornuta* the chief governing factor is rate of flow of the water, the former preferring rheocrene (stream) and the latter limnocrene (pool) conditions. Temperature also affects the competition between these two species, *Planaria alpina* preferring the colder temperatures. But when limnocrene conditions extend up to the spring head into the preferred temperature the latter species, *Polycelis cornuta* either replaces or exists together with it right up to this point. Beauchamp (1932) studied the influence of ecological factors on the competition between stream and lake-living triclads. Stream forms are sometimes washed down and are capable of colonizing stony areas. *Planaria alpina* is confined to the 'Brandungszone' because among other reasons it there avoids the competition of *Polycelis nigra* with which it cannot live in close competition and which probably devours it.

According to Elton (1927, pp. 36–8) the copepod crustacean *Eurytemora lacinulata* cannot live together with another copepod *Diaptomus gracilis* in the same ponds, although it may be found in similar and neighbouring ponds from which *D. gracilis* is absent. Gause (1934, p. 22) quotes observations by Kessler and by Birstein and Vinogradov on the extermination of the broad-legged crayfish *Potamobius astacus* by the long-legged *P. leptodactylus* when the latter were introduced into lakes naturally inhabited by the former. Wilson (1917: quoted from Pearse, 1939, p. 522) states that learnaepodid crustaceans and the glochidia of clams are, as a rule, mutually exclusive when parasitizing fishes, but that a light infestation with one parasite may not be sufficient to keep off the other. On the other hand, commensals which do not compete may often occur together on the same 'host' (Pearse, 1939, pp. 504 et seq.).

(e) Insects

(1) *Cultures of granivorous insects.* The competition occurring at all stages of the life cycle between different species of granivorous insects has been analysed in detail (Crombie, 1942, 1943, 1944a, 1945, 1946). Several features led to the choice of these organisms for such an investigation. Their biology was already known with reasonable accuracy. A number of different species inhabit the same environment and are thus suitable for studies in interspecific competition. They breed rapidly and adults and juvenile stages live on the same food. Their food supply is easily regulated and the physical conditions of their environment kept constant. Finally, changes wrought in the medium by the organisms themselves are comparatively easily controlled. The species chosen were three beetles, *Rhizopertha dominica* (Bostrichidae) *Tribolium confusum* (Tenebrionidae) and *Oryzaephilus (Silvanus) surinamensis* (Cucujidae) and one moth, *Sitotroga cerealella* (Gelechiidae). The adults of the beetles live for several months, a period several times longer than the generation time, and following copulation the females oviposit fertile eggs more or less continuously during most of their adult lives. Male and female longevities are approximately equal. Both adults and larvae of *Tribolium confusum* and *Oryzaephilus surinamensis* feed in the open medium, e.g. crushed wheat or flour, but pupation tends to occur in crevices. The adults of *Rhizopertha dominica* feed in the open medium, but the larvae bore into wheat grains or other food materials (through crevices in which they can get the necessary leverage) and complete their development inside. The adults of *Sitotroga cerealella* live for only a few days or weeks, a period shorter than the generation time. Upon copulation, the females lay nearly all their eggs within a few days.

The habits of the larvae are very similar to those of *Rhizopertha dominica*.

In insects, fecundity determines the upper limit of natality, defined as the rate of emergence of adults. But this is seldom achieved. Infertility in the eggs, and mortality in the egg, larval and pupal instars all contribute to its reduction. As the adult is the only instar capable of reproduction in most insects, the rate of oviposition of the whole population will depend upon the number of fertile females present and upon their average fecundity (rate of oviposition). Population growth will then be governed by the factors affecting natality, sex ratio and adult longevity, natality itself being determined by fecundity, the fertility of the eggs, and egg, larval and pupal mortality. If physical conditions remain constant and the organism itself does not change, all changes in these factors will be density-dependent. Crowding may then affect population growth through the limitation of (1) food or oxygen, or (2) space (leading to reflex stimulation caused by the presence of other individuals), or (3) the accumulation of metabolic waste and other products ('conditioning' of the medium). When precautions were taken to prevent the conditioning of the medium and to maintain the food supply at a constant level, competition for space, whether intraspecific or interspecific, played the most important role in determining the rate of population growth of these insects. This factor usually prevented the ratio of population to food supply reaching a value at which the latter would be insufficient. Oxygen lack was never observed. When the medium was allowed to become conditioned, such conditioning quickly rose to paramount importance and dominated population growth. The incidence of all these factors was upon natality, the sex ratio being never and adult longevity never importantly affected. Egg-fertility was also never affected.

In unconditioned wheat media, at densities possible in actual populations, reduction in fecundity of *Rhizopertha dominica*, *Sitotroga cerealella* and *Oryzaephilus surinamensis* was entirely due to competition for space for two purposes: oviposition and feeding in the two beetles, and for oviposition only in the moth (Crombie, 1942). Crowding thus affected fecundity through behaviour, and when two species were inhabiting the same environment their mutual effect upon each other's fecundity was greater in proportion to the similarity of their oviposition sites. It is crowding in relation to oviposition sites (e.g. the number of adults per wheat grain) and not crowding in relation to total space, which affects their fecundity. This seems to imply that the females of these species perceive their oviposition sites as such. The nature of this perception in *Rhizopertha dominica* has been analysed (Crombie, 1941). Scarcity of oviposition sites upsets the normal oviposition rhythm of

R. dominica and *Oryzaephilus surinamensis*, and leads the females to deposit their eggs in unusual places. While oogenesis in these two species is evidently adapted to a continuous although not complete restraint from oviposition while crowding is intense, in *Sitotroga cerealella* this is not so. An initial restraint is followed by a sudden burst of oviposition, due presumably to the pressure of egg production. But complete restraint may be exercised. The stimulus to oviposition in this species is tactile, depending on the presence of crevices. The females will die full of eggs rather than oviposit them in an empty glass dish which does not provide this stimulus. In unconditioned flour media reduction in fecundity of *Tribolium confusum* and *Oryzaephilus surinamensis* was also brought about by the competition for space, as was their mutual effect on each other when these two species inhabited the same medium (Crombie, 1943). In conditioned media the fecundity of all three beetles was reduced more or less in proportion to the degree, and irrespective of the species causing the conditioning. This effect seems to be due rather to 'poisoning' than to starvation, and is one of short duration upon oviposition rather than a lasting effect upon egg production (Crombie, 1942, 1943).

The behaviour of the ovipositing females is not well adapted to the care of the young. Although the rate of oviposition is reduced by crowding, it remains so high that a considerable mortality must occur in the immature stages before the offspring are reduced to numbers within the capacity of the environment to support them. The fate of the supernumerary young of *Tribolium confusum* and *Oryzaephilus surinamensis* is to be destroyed by adults and larvae (Crombie, 1943; Stanley, 1941, 1942, 1943). Eggs are destroyed in direct proportion to their density and the density of feeding stages present, and the same relationship may be supposed to hold for the destruction of pupae. In unconditioned media destruction of the young stages, particularly by the adults, is so much the most important factor reducing natality that the others may be ignored. This and the rate of oviposition alone determine the rate of population growth of each of these species, and the relative rates at which each destroys the young stages of the other also determines the result of competition between them. Here the less voracious and equally vulnerable *O. surinamensis* is at a considerable disadvantage. It does not attack the pupae of *Tribolium confusum* at all, and attacks its eggs at a lower rate than its own eggs are attacked by *T. confusum*. Any egg of the latter species which hatches is thus safe from *Oryzaephilus surinamensis*, while the latter, whose pupae are attacked by *Tribolium confusum*, is not safe from its rival until it emerges as an adult. In conditioned media larval and pupal mortality and the duration of the larval stage of *T. confusum* are, as Park (1938) and

Park, Miller & Lutherman (1939) have shown, more or less proportional to the degree of conditioning, while eggs are unaffected.

At the highest densities reached in growing populations of *Rhizopertha dominica* and *Sitotroga cerealella* fecundity remained almost at its maximum (Crombie, 1944a). This means that the larvae must be adapted, particularly during the early instars, to an independent existence. They show an ability both to choose, by means of a chemical sense, objects composed of suitable food in which to develop and to avoid overcrowding by migrating from such objects (e.g. wheat grains) containing other larvae. The latter seems to be caused entirely by encounters within the wheat grain. There is no evidence that larvae perceive each other at a distance. Such encounters occur at random and result in fighting, followed by death or migration. This is entirely a competition for space. It occurs at densities far below that at which food would become scarce. With both species the average number of adults emerging per grain is 1·2 when larvae in any number greater than one enter a grain, whereas there is enough food present per grain to support approximately 4·5 *Rhizopertha dominica* and 3 *Sitotroga cerealella*. Among larvae of the same age neither conditioning of the medium nor lack of oxygen come into effect. It is probably for these reasons that larval crowding has no effect upon the size or fecundity of the adults into which they grow.

Except for a small unexplained 'intrinsic' mortality among the larvae of *Sitotroga cerealella*, larval mortality is entirely density-dependent and is the result of random encounters. With a limited number of wheat grains of course those migrating would merely die elsewhere. The probability that any particular larva will survive is then inversely proportional to the initial number i present, but the average number of larvae a which complete their development in one wheat grain remains constant at all values of i greater than l . Where P represents the proportion dying, the relationship between survival and density, expressed as the number of larvae per grain, is thus given by the equation $(1-P)=a/i$. This relationship, which when survival is plotted against density is hyperbola-like, holds for both species alone and in competition. In all cases $a=1\cdot2$. In interspecific competition between larvae, *Rhizopertha dominica* has a greater relative rate of survival than *Sitotroga cerealella* in the proportions 1·3*R*:1*S*. Mortality is greater the nearer the competing larvae are to the same age, the older usually standing at an advantage. With sufficient differences in age the number of larvae completing their development per grain rises above 1·2. In *S. cerealella* a certain proportion of larvae have atypical rates of development which thus enable them to survive competition for

space and take advantage of the available food supply where normal specimens would succumb. Since *S. cerealella* females lay large batches of eggs during a single bout of oviposition, e.g. upon one ear of wheat in the field, this feature of their biology probably increases their survival in nature. Mortality during the immature stages due to larval competition is thus by far the most important factor reducing natality in these two species, and with the rate of oviposition it may be considered to determine the rate of population growth of each species alone and in competition with the other.

This analysis of the factors determining the rate of population growth may now be used to explain the observed growth of populations of each species alone and in competition with others under controlled conditions (Crombie, 1945, 1946). Populations of each species alone began with a small number of individuals and competing species began with various initial numerical relationships. In flour, which is suitable for the development of *Tribolium confusum* and *Oryzaephilus surinamensis*, changes in the numbers of all instars could be observed by sieving the medium. This could not be done with *Rhizopertha dominica* and *Sitotroga cerealella* which require a different type of medium, e.g. wheat in the grain. In the latter only adults could be counted and changes in the immature instars were inferred from the detailed analysis already described.

Populations of each species living alone in media containing a limited food supply which was allowed to become conditioned, increased to maxima and then declined as the food became exhausted and waste products accumulated. As time passed the age composition of *Tribolium confusum* and *Oryzaephilus surinamensis* populations shifted from a majority of young stages to a majority of adults (Crombie, 1946). The decline of the populations was due mainly to the failure of the larvae to develop and pupate, but in *O. surinamensis* the cessation of oviposition also contributed to this effect. The size of *Sitotroga cerealella* adults decreased in succeeding generations and the longevity of *Rhizopertha dominica* was also reduced in conditioned media.

In media in which the amount of food was maintained at a constant level and conditioning was prevented, the adult populations of each of the four species rose to a maximum which was independent of the initial population and remained indefinitely fluctuating about this value. The adult populations of *Sitotroga cerealella* fluctuated violently because adults died before those of the next generation had emerged. The maxima were always below those which the food present could support and were therefore presumably determined by competition for space. A comparison of the rates of oviposition with the rates at which adults emerged showed that in the maximum

populations there was an immense mortality in the immature stages. This amounted to over 90% with *S. cerealella* and over 99% with each of the other three species. The intensity of selection thus increased from a low value at the beginning of population growth to a very high value at the end.

Interspecific competition in unconditioned media was chiefly for space, whereas in media which began with a limited food supply which was not renewed it was chiefly for food, with conditioning as a contributory factor. As a result the competitive relationship between two species was sometimes different in the two kinds of medium, e.g. the competitive relationship between both *S. cerealella* and *Rhizopertha dominica*, and *Oryzaephilus surinamensis*, 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 *O. surinamensis* 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 the latter remained the same in both media.

Species occupying different ecological niches survived together in the same medium while of those occupying the same niche one always exterminated the other. The results of competition in unconditioned media between different combinations of species are shown in Table 1. *Rhizopertha dominica* always eliminated *Sitotroga cerealella* from media of wheat because their larvae have similar needs and habits and those of the former species are intrinsically superior. *Rhizopertha dominica* thus excels *Sitotroga cerealella* in interference and it also does so in rate of reproduction and survival. Each generation of *S. cerealella* adults dies quickly, leaving its offspring as the sole representative of the species, whereas the gains made by each generation of *Rhizopertha dominica* larvae accumulate in the long-lived adults whose continuous oviposition gives succeeding generations of its larvae a tremendous majority, until *Sitotroga cerealella* decreases to zero. *Tribolium confusum* always eliminated *Oryzaephilus surinamensis* from media of flour where all individuals were equally open to attack. The former species excells the latter in interference (destruction of immature stages) and it also has a higher rate of reproduction and survival. But in crushed wheat and in flour containing pieces of glass tubing of a bore large enough for the larvae of *O. surinamensis* to enter and pupate in, but too small for the larvae of *Tribolium confusum*, the former species was able to survive side by side with the latter. With glass tubing of wider bore which *T. confusum* adults can enter, *Oryzaephilus surinamensis*

was exterminated as in plain flour. In wheat *Rhizopertha dominica* and *Sitotroga cerealella* survived together with *Oryzaephilus surinamensis*, and *Rhizopertha dominica* with *R. confusum*, because the larvae of the first two species develop and feed inside the grains and so avoid destruction by the adults and larvae of their competitors which feed in the open medium.

It is always convenient and may be instructive to express the results of a long series of observations in the form of a compact algebraic equation. If such an equation be merely empirical, it will be useful according as the accuracy with which it describes the observations themselves, and as the range over which it holds good increases. If it is to be more than empirical, then each of the parameters must represent a factor actually operating in nature (Gray, 1929).

Table 1. Results of competition between species according to ecological niche (unconditioned media)

	<i>Sitotroga cerealella</i>	<i>Oryzaephilus surinamensis</i>	<i>Tribolium confusum</i>
<i>Rhizopertha dominica</i>	<i>R.</i> exterminates <i>S.</i> in wheat: larvae similar, <i>R.</i> superior	Both survive in wheat: immature <i>R.</i> protected, <i>O.</i> not attacked	Both survive in wheat: immature <i>R.</i> protected, <i>T.</i> not attacked
<i>Oryzaephilus surinamensis</i>	Both survive in wheat: immature <i>S.</i> protected, <i>O.</i> not attacked		<i>T.</i> exterminates <i>O.</i> in flour: both eat immature stages but <i>T.</i> more voracious. Both survive in crushed wheat, or flour with tubing which protects <i>O.</i> pupae

Populations of *Sitotroga cerealella* are separated during growth into distinct generations, but population growth may be measured by considering only the sizes of successive generations of adults. With this adjustment, adult population growth of this species and of *Rhizopertha dominica* is determined by a statistically constant rate of oviposition and one overwhelmingly important density-dependent check, larval competition. Although, as shown above, the relationship between larval mortality and larval density is not linear, at the very high larval densities present this relationship does hold to a first approximation. At such densities, since the rate of oviposition may be considered unchanged, larval mortality is also approximately linearly related to adult population density. In the Verhulst-Pearl 'logistic' equation, population density is related to time by a constant representing the rate of reproduction and by a factor which reduces this in direct proportion to population density (Crombie, 1945). Two simultaneous logistic equations (the Lotka-Volterra equations) may be used to describe the growth of two species competing for the same limited environment, by the introduction of two other parameters ('competition coefficients') representing the notion that each species inhibits the increase of the other as a function of its own density.

Here the function is assumed to be linear (Lotka, 1925, 1932; Volterra, 1926; Kostitzin, 1937; D'Ancona, 1942). In these experiments, these two species do to a first approximation inhibit each other's increase in this way, a single parameter in each equation representing the overwhelmingly important factor determining competition, the struggle between the larvae. The parameters of the logistic equation and the Lotka-Volterra simultaneous equations are thus to a first approximation related to each other in the same way as the biological processes which they represent, and these equations describe adult population growth with an accuracy commensurate with that of the observations. But because of the variability of the biological processes the experimental error is large. The biological assumptions of these equations are also not strictly true for *Tribolium confusum* and

Oryzaephilus surinamensis. The rates of oviposition of these species are statistically constant; but since the checks to their increase depend on encounters between feeding (adult, larvae) and eaten (pupae, eggs) instars, these are related to population density not by a linear but by a quadratic factor (Crombie, 1946). But the divergence between the actual relationship between survival and density and the linear relationship assumed by the equations is no greater than the experimental error due to the variability of the rates of destruction of eggs and pupae. When 'competition coefficients', calculated from the observed relationships between density and the relative rates of destruction of the immature stages, were inserted into the Lotka-Volterra simultaneous equations, the latter were found to describe the growth of the competing populations in a rough way. Equilibrium positions which are independent of initial population densities were reached by populations of all the pairs of competing species studied. These equilibrium positions are described to varying degrees of accuracy by the Lotka-Volterra simultaneous equations (Figs. 1, 2 and 3).

In Park, Gregg & Lutherman's study (1941 of the competition between the beetles *Tribolium confusum*, *Gnathocerus cornutus* (Tenebrionidae) and *Trogo-*

Interspecific competition

Trogoderma versicolor (Dermestidae) in a medium of fine flour, coarse rolled oats and yeast, the outcome of competition often depended on the initial concentrations of the competing species (Park, 1943). Thus, when *Tribolium confusum* got well established it always drove out *Gnathocerus cornutus*, but when *Tribolium confusum* adult population was reduced to a low value, apparently by an epidemic protozoan

densities of *Gnathocerus cornutus* this species always exterminated *Trogoderma versicolor*. *Gnathocerus cornutus* seems to inhibit (perhaps by predation) the pupation and emergence of the latter. When *Trogoderma versicolor* had the initially higher density, *Gnathocerus cornutus* was exterminated. The values of the constants of the Lotka-Volterra simultaneous equations roughly calculated for these two species

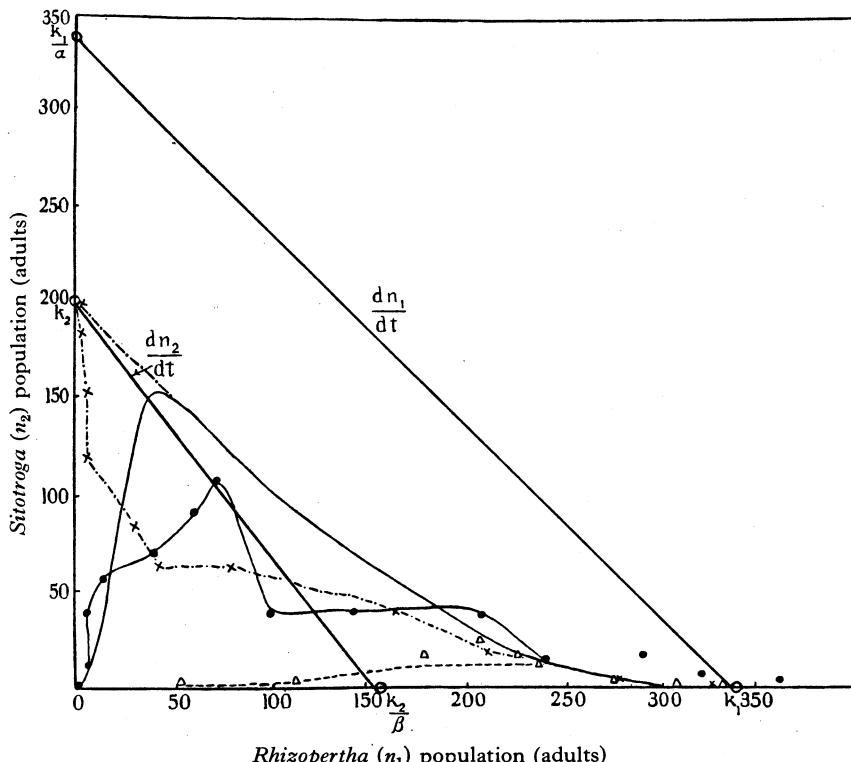


Fig. 1. Diagram illustrating the competition between *Rhizopertha* (n_1) and *Sitotroga* (n_2) in renewed wheat, with different initial concentrations. The theoretical curves were calculated from the Lotka-Volterra simultaneous equations. Two *Rhizopertha* versus 2 *Sitotroga*: ●—● (observed), —— (calculated); 50 *Rhizopertha* versus 2 *Sitotroga*: △—△ (observed), ----- (calculated); 2 *Rhizopertha* versus 200 *Sitotroga*: ×—×—× (observed), - - - - (calculated). The two broken theoretical curves eventually join the full theoretical curve. The *Sitotroga* were always exterminated.

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

(Figure reproduced from Crombie (1945), Proc. Roy. Soc. B, 132: 362-95, Fig. 2, by permission.)

infection, this species was exterminated by superior numbers of *Gnathocerus cornutus*, which apparently eats its eggs, small larvae and pupae. If the *Tribolium confusum* adult population had not undergone violent oscillations it seems probable that it would always have exterminated *Gnathocerus cornutus*. *Tribolium confusum* always exterminated *Trogoderma versicolor*, irrespective of initial imaginal densities, at a rate roughly proportional to the initial concentration of the former species. With equal or superior initial

(see Crombie, 1946) usually correspond to the fourth condition of equilibrium (Crombie, 1945), where the inhibition of each species by the other is greater than its auto-inhibition, and it is initial densities which chiefly determine which species could survive together in the same environment. But the nature of the competition between them has not yet been fully analysed. When all three species competed (with equal initial numbers) the *Trogoderma versicolor* population fell steadily to zero after 90 days, and

Gnathocerus cornutus disappeared next after 510 days, leaving *Tribolium confusum* alone. (See p. 73.)

Two other examples of interspecific competition may be mentioned here. MacLagan (1932) found that competition between the moth *Sitotroga cerealella* and the grain weevil *Sitophilus granarius* (Curculionidae) reduced the rate of reproduction of each species. Vladimerova & Smirnov (1938, cited from Park, 1941) found that interaction between two species of house-fly stimulated the population growth of one while depressing that of the other.

(2) *Insect parasitoids*. Examples of interspecific competition are found among the larvae of insect parasites and parasitoids (Clausen, 1940) which commit multiparasitism in their hosts—the eggs, larvae or pupae of other insects. This, as Imms (1937) points out, usually occurs when the ovipositing females fail to distinguish parasitized from unparasitized hosts, and so depends upon an error of instinct. This occurs sometimes with the hymenopterous parasites of the moth *Plutella maculipennis* (Lloyd, 1940). In his review of this subject Imms (1937)

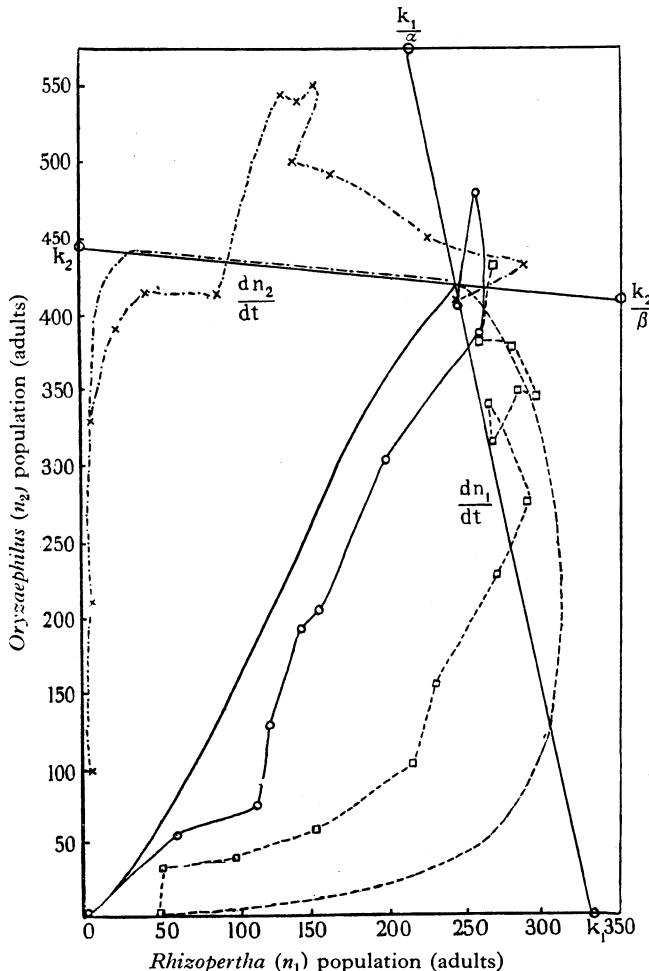


Fig. 2. Diagram illustrating the competition between *Rhizopertha* (n_1) and *Oryzaephilus* (n_2) in renewed wheat, with different initial concentrations. The theoretical curves were calculated from the Lotka-Volterra simultaneous equations. Two *Rhizopertha* versus 2 *Oryzaephilus*: ○—○ (observed), —— (calculated); 50 *Rhizopertha* versus 2 *Oryzaephilus*: □—□ (observed), --- (calculated); 2 *Rhizopertha* versus 100 *Oryzaephilus*: ×—× (observed), - - - (calculated). Both species survived together and their populations reached the same equilibrium point whatever the initial values (Crombie, 1945).

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

(Figure reproduced from Crombie (1945), Proc. Roy. Soc. B, 132: 362-95, Fig. 7, by permission.)

Interspecific competition

distinguishes three categories: where only one species of parasite survives, where both survive and where none survives. Those in the last category usually die through lack of food. The winner in the first category is frequently the one which first attacks the host and so reaches the destructive feeding stage before its rivals. Parasite larvae frequently attack one another within the host, while others kill rivals by toxic secretions. The competitive relationship between species in the second category calls for special investigation: little is known about them.

During competition between the solitary hymenopterous parasites *Pteromalus puparum* and the gregarious *Hemiteles melanarius* (Martelli, 1907) or *Pimpla instigator* (Picard, 1922), the latter were always exterminated. *P. instigator* was also destroyed by the tachinid fly *Compsilura* which eats the organs of the host (the cabbage white butterfly (*Pieris brassicae*)) before pupating. Parker (1933) found that when the hymenopterous parasites *Anastatus disparis* and *Oenocyrtus kuvanae* both attacked the same egg of their host (the gipsy moth, *Porthearia dispar*) either both

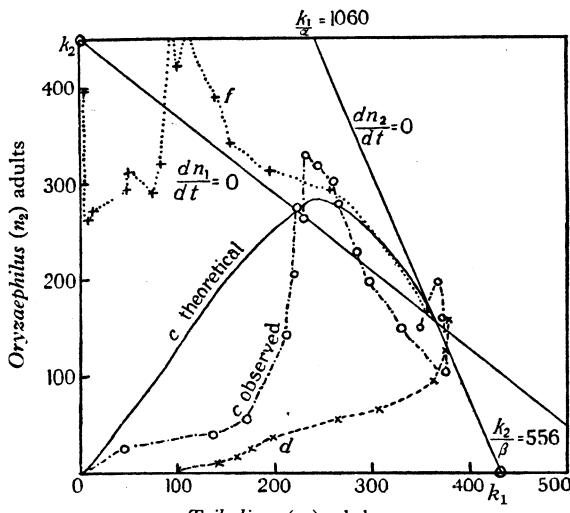


Fig. 3 (a)

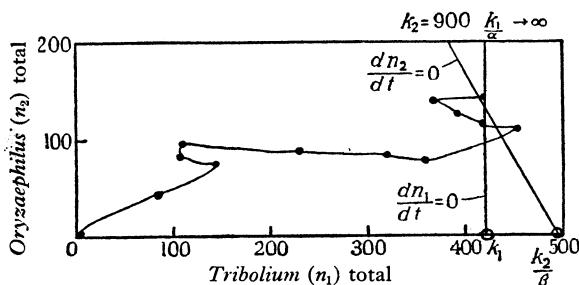


Fig. 3 (b)

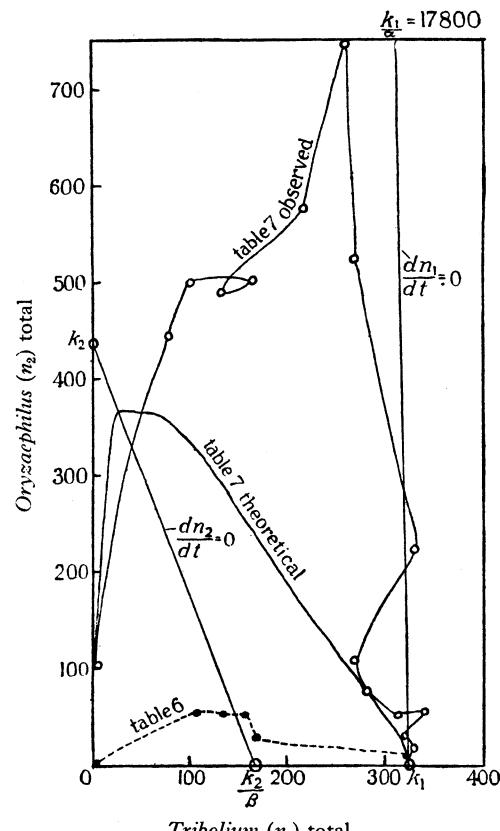


Fig. 3 (c)

Fig. 3. Diagrams illustrating the competition between *Tribolium* (n_1) and *Oryzaephilus* (n_2) in various renewed media, with different initial concentrations. (a) Wheat: the curves represent respectively changes in adult populations which began with the following initial values: 4 *Tribolium* versus 4 *Oryzaephilus* (curve c); 100 *Tribolium* versus 4 *Oryzaephilus* (curve d); 4 *Tribolium* versus 400 *Oryzaephilus* (curve f). (b) Fine flour with 1 mm. bore glass tubing: the curve represents changes in total populations (eggs, larvae, pupae and adults) beginning with 4 adults of each species. (c) Fine flour: the curves represent respectively changes in total populations which began with the following initial values: four adults of each species (Table 6); 4 *Tribolium* and 100 *Oryzaephilus* adults (Table 7). The theoretical curves were calculated from the Lotka-Volterra simultaneous equations. In (a) and (b) both species survived together and their populations reached the same equilibrium point whatever the initial values. In (c) the *Oryzaephilus* were always exterminated (Crombie, 1946).

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

(Fig. reproduced from Crombie (1946), Proc. Roy. Soc. B, 133: 76-109, Fig. 10, by permission.)

parasites died before reaching maturity or *Anastatus disparis* survived alone if it attacked the host while its rival was in an early larval instar. But in the field there would be no serious competition between the total populations of the two species unless the parasitism approaches the limit of the available host eggs. According to Smith (1933) the larvae of the hymenopteran *Scutellista cyanea* preys on the eggs of the black scale *Saissetia oleae*, which are found beneath their parent's body. When the former insect was introduced from South Africa into California the native hymenopteran *Tomocera californica*, which has almost identical habits with *Scutellista cyanea*—its larvae also feeding on the eggs of *Saissetia oleae* beneath the parent scale (Clausen, 1940, p. 210), was almost although not entirely eliminated.

(3) *Field observations.* Lloyd, Graham & Reynoldson (1940) and Lloyd (1943a, b) studied, by continuous trapping for several years, the competition occurring between several species of dipterous larvae and a worm in sewage beds. The fauna of these bacteria beds is a balanced one and comprises in particular the oligochaete worm *Lumbricillus lineatus* (Enchytraeidae), the flies *Psychoda* spp. (Psychodidae), *Metriocnemus* spp. and *Spaniotoma minima* (Chironomidae). The seasonal abundance of the different species depends chiefly on the weather which influences *Metriocnemus longitarsus* and *Lumbricillus lineatus*, the dominant forms in the upper region of the bed, and these affect the other species by competition. Weather also directly affects the subordinate forms. There are three lines of evidence for competition. First, the expected monthly abundance was calculated from the speed of life cycle at different temperatures and compared with the actual abundance. In spring and early summer the *Psychoda* are most abundant, but from about May their numbers fall below the expected figures. This coincides with the abundance of *Metriocnemus*, *M. longitarsus* larvae forming a barrage in the upper layers, followed by the midsummer maximum of *Spaniotoma minima* when *Metriocnemus longitarsus* declines because of its habit of feeding and pupating near the surface where it suffers from drying. *M. hirticollis* has a major flight slightly later than *M. longitarsus*, and so is also dependent for its summer establishment on the number of the latter. In autumn *M. longitarsus* again increases, causing a decline in *Spaniotoma minima* below its expected numbers and preventing any increase in the *Psychoda*. Secondly, in a neighbouring sewage works from which the *Metriocnemus* were absent and where (probably because of the lack of competition from them) *Spaniotoma minima* reached its maximum later, the summer depression of the *Psychoda* was much less pronounced. Thirdly, differences in the relative abundance of the flies in different parts of the beds are determined to some

extent by the sweeping action of the sewage distributor. The *Psychoda* larvae tend to occur most abundantly in parts not favoured by the chironomids, although in the absence of the latter their distribution would be more uniform. Also, although the *Psychoda* larvae prefer the upper layers of sewage in the neighbouring works where the *Metriocnemus* are absent, in the presence of these organisms (which also prefer the upper layers) the *Psychoda* are found in greatest density below this zone. Where the larvae of *Spaniotoma minima* are reduced in the depths by the abundance of *Metriocnemus longitarsus* larvae the psychodids, which probably always oviposit to some extent there, are able to extend their period of abundance later in the year. The chief element in competition seems to be the predatory tendency of the chironomid larvae. This is in keeping with the structure of the mouth parts. Most of the destruction occurs to the eggs. Besides such direct attacks the larvae and the worms affect each other during grazing by loosening eggs, pupae and worm cocoons from the medium. Over-population may occur locally at some seasons of the year. Evidence of competition for food is found in the increased mortality of *M. longitarsus* and a reduction in weight of the emerging flies of this species and of *Spaniotoma minima*. *Lumbricillus lineatus* enters chiefly as a competitor for food, particularly after warm winters when it breeds more rapidly and causes an earlier spring deprivation for the larvae of *Metriocnemus longitarsus* and *Psychoda severini*.

Ecological succession of insect species in carcasses has been observed by Holdaway (1930) and Fuller (1934). These authors believe that the succession of dominant species is determined by two factors, first, the changes going on in the carcass itself, each stage of decomposition being characterized by a particular group of insects, and secondly, by competition. With the flies competition occurs chiefly among the larvae and often limits the niche they occupy (Evans, 1936). Interspecific interference apparently reduces the generation size of tsetse flies, *Glossina* spp. (Jackson, 1945). In a review of insect outbreaks in Europe Carpenter (1940) states that fluctuations in population are a general phenomenon of a large area. While fluctuations in the population as a whole cannot be characterized by any individual species, in years when a larger insect population occurs there is great upsetting of the biotic balance. This is shown by the decrease or increase in numbers of species which have characteristically prolonged periods of outbreak. Very often concurrently outbreaking species fall into the same ecological niche. Then in subsequent outbreaks in the same area the same species may not always take the lead, but one of the former subordinate species may reach the greatest abundance.

(4) *Drosophila mutants*. Finally, attention may be drawn to competition between different species or genotypes of *Drosophila*. Morgan & Tice (1914) observed that the expected hereditary ratios in *Drosophila* populations were changed by overcrowding, probably by differential mortality in the immature stages (Hammond, 1939). Timoféeff-Ressovsky (1933, 1935) studied experimentally the competition in artificial media between *D. melanogaster* and *D. funebris* and between races of the latter from different geographical regions. In mixed cultures of larvae the relatively more successful was the species or race the temperature of whose natural habitat corresponded most closely to that at which the experiments were conducted (Timoféeff-Ressovsky, 1940). Gagarin (1933, cited from Bodenheimer, 1938, p. 147) found that in mixed populations of *Drosophila* nearly all the mutants are eliminated by the wild type after a few generations. L'Héritier (1937) reviews the physiological differences between different allied species, especially of *Drosophila*, and describes experiments designed to study the hereditary basis of such differences. Different hereditary lines of wild type *D. melanogaster* were put in competition with various mutants from which they are distinguishable morphologically. Food was exposed to the simultaneous oviposition of the two competitors and competition occurred among the larvae. When oviposition was not simultaneous the eggs laid first had the greater chance of becoming adults. The relative success of the different lines was the same when competing with any of the mutants and corresponded to the order of resistance of the adults to starvation. L'Héritier & Teissier (1935) studied the competition between *D. melanogaster* and *D. funebris* in artificial media with a constant food supply and found that, whatever their initial concentrations, equilibrium was established with a large population of the former and a small one of the latter species. But the precise part of the food for which competition occurred is not known (Robertson & Sang, 1944a, b). Cheruwimov (1932) and L'Héritier & Teissier (1937) studied under experimental conditions, and Olenov *et al.* (1937) and Gordon (1939) by releasing mutants among natural populations, the rate of elimination of certain forms. Their results do not fully agree, some finding that the mutants disappeared altogether and some that they maintained themselves in a balanced population with the wild type. The conditions of competition here need further investigation.

(f) Vertebrates

A number of examples are described in §3 where differences in structure, habits or distribution between congeneric species of vertebrates may, according to

the argument developed in §1, be attributed to competition, or where competition may be inferred from the fact that the animals eat the same food. There seem to be comparatively few direct observations of interspecific competition in this group. Gause (1934) quotes an example of competition among fish described by Kashkarov. When the wild carp, *Cyprinus albus*, was introduced into lakes inhabited by *Schizothorax intermedius*, the latter was gradually eliminated because the carp eats its spawn. The competition of introduced species for the same resources seems to have been at least partly responsible for the disappearance of native species of fish, birds and mammals in New Zealand, although it is difficult to separate this from the undoubtedly effect of introduced predators and the disturbance of habitats by man (Thompson, 1922). Formosof (1933) claimed that decreases in squirrel numbers in Siberia correspond to invasions of the Siberian nutcracker, *Nucifraga caryocatactes macrorhynchos*, which competes for the same food. In Britain at the present time the native red squirrel, *Sciurus vulgaris*, appears to be decreasing rapidly before the introduced grey squirrel, *S. carolinensis*. The black rat, *Rattus rattus*, seems to have suffered in the same way from the competition of the brown rat, *R. norvegicus*, in temperate Europe. The former is considered to have been imported into Europe from Asia at the time of the Crusades and became a serious pest during the Middle Ages. The brown rat, also from the East, invaded Europe in the eighteenth century and, corresponding to its increase, the black rat has practically disappeared from temperate latitudes to which it is less well adapted than its rival, while in warm climates and in environments where its superior climbing ability is an advantage (e.g. in buildings) it apparently holds its own (Barrett-Hamilton & Hinton, 1910-21; Hinton, 1918).

3. DIFFERENCES IN DISTRIBUTION, STRUCTURE AND HABITS ATTRIBUTABLE TO COMPETITION

In many of the examples given of competition between species with similar ecology, neither the factors controlling population density nor the ecological relations between the competitors are accurately known. But where these details have been investigated, it proves that, in keeping with the theoretical demonstration set out in §1c, species with the same needs and habits cannot survive together in the same place when the ratio of population density to environmental resources reaches a value at which competition occurs. Such species are not necessarily taxonomically related. This principle, as Darwin has pointed out, is likely to have two kinds of effects on organisms in nature: (1) on their dis-

tribution and abundance, and (2) on their evolution. Two important points raised by this survey need special emphasis. The first is the necessity of making often the most detailed study of the needs and habits of an organism. Often the very slightest differences, birds feeding at slightly different levels of the vegetation or at slightly different times or small differences in food preferences, may enable species in other respects very similar to survive together (Vestal, 1914). The second point is that adaptive differences between related species (or races) are often not in evidence until competition between them has been observed (Lack, 1944).

(a) *The effect of interspecific competition on distribution and abundance*

The importance of interspecific competition in ecological succession has already been mentioned, and Beauchamp & Ulyott (1932) have shown how it may affect the distribution of organisms in nature. Elton's (1944, 1946) study of 'fifty sample surveys in widely different habitats and parts of the world' suggests that it may determine the structure of animal communities.* He found 'a rather constant relationship between the number of species and the number of genera present. This relationship suggests that species belonging to the same genus tend strongly not to occur in the same area of any major habitat at the same time; that this is attributable to competition for resources available in a particular ecological niche; that apart from this, the main extra-specific ecological relations between animals in a community are those between genera; that the genera chosen by the majority of taxonomists are ecological realities; and that, as previously indicated by the limited numbers of species in an animal community, the latter is an organization with strictly limited membership determined by very definite laws. From this hypothesis it would follow that the successful introduction of a new species will usually cause the decrease, often disappearance, of one of the species already present. The empirical relationship established here for the relation of species to genera seems to apply also to plant associations' (Elton 1944; see also de Candolle, 1820 and Darwin, 1859, p. 115). An analogous explanation may help to account for the definite relationship often found between the number of species and the number of individuals in a random sample of an animal population. Garthside (cited by Chapman, 1931, p. 398, and Graham, 1933) and Fisher, Corbet & Williams (1943) found that while a few, often only one, insect species are characterized by a large number of indi-

viduals, most occur in relatively small numbers. Lloyd, Graham & Reynoldson (1940) and Reynoldson (1942) observed the same phenomenon in bacteria sewage beds, where one species dominated the insect fauna and the fungus flora respectively. Gause (1936) refers to the same relationship among plants (cf. Jaccard 1912, 1941) and other organisms. Such a definite relationship between the numbers of different species in a given environment could be brought about either by some regularly acting environmental factor or by interaction between the species themselves. Interaction could bring about such a relationship in two ways. The numerous rare species may create a favourable environment for the few numerous species, or the latter may behave as dominants and by competition eliminate the rare species from all but a few ecological niches in which they can hold their own. Whether either of these explanations is correct or not, the subject would repay investigation.

(b) *Interspecific competition and evolution*

Reproductive isolation between different members of a species, leading to the formation of new species, seems to be initiated in at least two different ways: by genetic changes and by some form of geographical or ecological isolation. The evolutionary role of competition between the divergent forms varies according to whether they interbreed or not.

(1) *Reproductive isolation initiated by genetic factors.* Mayr (1942) uses the term 'instantaneous sympatric speciation' to designate 'the production of a single individual (or the offspring of a single mating) which is reproductively isolated from the species to which the parent stock belongs. Such an individual would be the potential ancestor of a new species.' Several processes are known among plants, e.g. polyploidy of different kinds (Darlington, 1937, Dobzhansky, 1941), which would produce this result. Polyploidy is rare among animals since it interferes with the sex-chromosome mechanism (Dobzhansky, 1941), but Hogben (1940) has listed a number of methods by which instantaneous sympatric speciation could occur. These are: '(i) hermaphroditism combined with the possibility of self-fertilization, (ii) the existence of a separate spore-forming generation, (iii) parthenogenesis, (iv) production of individuals of either sex by clones from the same soma, (v) polyembryony, (vi) obligatory close-inbreeding, (vii) the occurrence of an epidemic of similar mutations at the same time. Restriction of the reproductive season and intense assortative mating in one form or another may also establish a partial species-barrier and enable species-differentiation to proceed by selection in the same environment from a different genetic basis. Such a barrier may gradually become a complete obstacle to interbreeding in the environment, and all stages

* [See, however, the paper by C. B. Williams (1947) in this *Journal*, 16: 11-18. Editor.]

of this process can be illustrated in moths' (see Darlington, 1940; Wright, 1940; Huxley, 1942; Mayr, 1942). Unless differences in needs and habits arise at the same time, it seems likely that, with the establishment of such breeding barriers, competition between the divergent forms will lead to the extinction of one of them. This seems to have happened among the Protozoa with different mating types already mentioned (Gause, 1942, see § 2(c)). Another example is the inter-tidal grass *Spartina townsendii*, an allotetraploid of the European *S. stricta* crossed with the American *S. alternata* (Huskins, 1931). *S. townsendii* is apparently superior to both parents, not only eliminating them in competition but extending its range beyond theirs (cf. Clausen, Keck & Hiesey, 1940, pp. 422–3). Similar examples are given by Huxley (1942, pp. 328 et seq., 386).

(2) *Reproductive isolation initiated by spatial isolation.* It seems likely that genetic divergence between two populations consisting of members of the same species is usually preceded by some form of geographical or ecological isolation (Robson & Richards, 1936; Dobzhansky, 1941; Huxley, 1940, 1942). Here, where at least at first genetically controlled breeding barriers are absent, a mutation is potentially able to enter into the genetic constitution of the whole species, and is only prevented from doing so by the mode of isolation in operation. Different authors place different emphasis on the roles of geographical and ecological factors in isolation. Lack (1940, 1944, 1945, 1947) believes that with birds new species have arisen primarily through geographical isolation, and that ecological isolation is enforced through competition when two species later meet in the same area. He argues against genetic divergence among birds arising out of ecological differences alone, that the latter do not provide sufficient barriers to inter-breeding. Mayr (1942) extends this objection to other organisms, remarking that in the absence of sexual isolation most forms of non-geographical divergence would be swamped by crossing between divergent forms (cf. Dobzhansky, 1941). But as Thorpe (1945) has recently pointed out, it is probably better to regard geographical, topographical and ecological isolation as different degrees of spatial isolation. Furthermore, this theoretical difficulty seems to have been overcome by the work of Mather (1943), who has shown that breeding barriers (isolation mechanisms) are likely to arise between any two populations where any factor—genetic, geographical, ecological or anything else—causes them to breed less freely with each other than each does within itself. After isolation mechanisms have arisen other differences between the two populations will accumulate, selection within each group tending to make each better adapted to its own habitat (in the sense of the parts of the physical and biological environ-

ment which affect it) than to that of the other. Members of each group would thus be at a disadvantage in the habitat of the other and competition between them with its consequent mortality will be greater the closer their needs and habits. There will therefore be selection both for differences in needs so that each makes different demands from the environment and for differences in habit, e.g. differences in behaviour, which tend to confine each to its own ecological niche. Such selection will continue until the two groups have diverged so far that competition no longer occurs.

After a careful study, Robson & Richards (1936) came to the view that it could not be concluded from the evidence available that differences in habit and structure between animal species are usually adaptive, adaptive differences appearing only between the higher taxonomic categories. The argument developed above makes it seem likely, however, that specific differences will be found to be usually adaptive. Lack (1944, 1945, 1947) has shown this to be true of many birds. As Lack (1944) points out, the presence of adaptive differences between closely related species of plants from different habitats is frequently very difficult to determine until one is transplanted into the natural habitat of the other, when it is usually quickly eliminated (cf. Sukatschew, 1928; Timoféef-Ressovsky, 1933, 1935). Circumstances under which random non-adaptive changes may accumulate in small populations have been described by Wright (1940). Another such circumstance would be if some factor such as predators or parasites kept a population of organisms in otherwise favourable circumstances more or less permanently below the density at which competition for environmental resources occurs, when the only form of selection would be for resistance to this factor. The survival of different variants would then be unrelated to their adaptive value in other respects and many of the differences between species originating thus may be unadaptive.

Whatever the cause of their divergence, related species which occur in the same area will tend to compete if the ratio of population to resources is high enough. It would then be expected that either one will completely eliminate the other from that area, resulting in geographical separation, or that they will survive together with some form of ecological isolation. The conclusion of Darwin's argument would thus be fulfilled. In fact, in all cases where such species have been studied, this conclusion proves correct.

Lack (1944, 1947) has made a survey of the ecological relations between congeneric species of birds on remote islands, in the finches of the Galapagos and in the passerine birds breeding in Britain. Related forms in the same area are thought to have met again after differentiation in isolation. In the

groups studied all related species, except for a few which need further investigation, reach one or other of the following stable positions. Either one species eliminates the other, or the two species occupy separate geographical regions or different habitats in the same region, or they live together in the same habitat and region but eat mainly different foods. The last is often achieved where the two species differ markedly in size. The type of ecological isolation found between two species may change seasonally or regionally. Lack (1945) studied the ecological relations between two related species of British non-passenger birds, the cormorant and the shag, which overlap in geographical range, and found that they differ markedly both in nesting sites and food. The same rule applies to German hawks and owls: no two congeneric species compete for food in the same habitat (Lack, 1946). Further, when species in different genera are compared, no two compete for the same food supply, with the apparent exception of the predators of the vole, *Microtus arvalis*. The latter forms the staple food of several species of hawks and owls, of which up to five (none congeneric) may occur together in the same habitat. The suggestion, which needs investigation, is made that these predators do not effectively compete with each other because for most of the time *Microtus* is superabundant, while when there is a vole minimum, each predator perhaps turns to a different prey. Gause (1934) quotes an observation by Formosov on four species of terns (*Sterna*) which nest together but differ in feeding habits. One feeds on land on insects, and the other three on fish, but they differ in size and the distance from shore at which they hunt. There are also examples among mammals, of which Lack (1944, 1945) quotes several, of differences in habitat and distribution which may be attributed to competition between related species, e.g. between the common hare *Lepus europaeus* and *L. timidus* and between the two European bank voles *Clethrionomys* (= *Evotomys*) *glareolus* and *C. nageri* (Barrett-Hamilton & Hinton, 1910-21). Similar examples of differences between congeneric species are cited by Huxley (1942, pp. 280 et seq.). Wilson (1907) observed that four species of Antarctic seals belonging to different genera live in the same habitat but on different food (see Bertram, 1940). Among amphibians, Noble & Evans (1932) remark that the selection of different habitats, due to different climbing abilities and avoiding reactions, enables the salamanders *Desmognathus f. fuscus* and *D. f. carolinensis* to avoid competition and inhabit the same area.

In his study of the gall wasp genus *Cynips*, which forms galls on oaks, Kinsey (1930), after examining 17,000 insects and 54,000 galls, came to the conclusion that (with one possible exception) in each

geographical area there is but one species (of the 93 into which he divides the genus) on any given species of host. The same rule applies to the 63 species of the gall wasp *Neuroterus* (Kinsey, 1923). In apparent contradiction with Kinsey (1930), Hogben (1940) remarks that 54 species of the family Cynipidae infest a single plant species (the oak). Several species of gall, sometimes of the same genus, 'are commonly found together on the same tree and the same leaf of the same tree'. But as no details are given it is impossible to tell whether the species in question make the same demands on the host and whether their populations reach sufficiently high densities for competition to occur.

Many examples of related species which differ either in distribution or ecology are given by Robson (1928), Thorpe (1930, 1940), Robson & Richards (1936), Diver (1940), Dobzhansky (1941), Huxley (1942), and Mayr (1942). Others seem to differ in neither fashion. These and other related species of organism living in the same area should be subjected to ecological analysis of the kind Lack (1944, 1945, 1946, 1947) has made with birds. Insects, about whose feeding and other habits a great deal of information has already been collected, would provide particularly suitable material for such a study. For instance, larvae of related species of Lepidoptera (Brues, 1920, 1936; Meyrick, 1928) and leaf miners (Hering, 1926; Needham, Frost & Tothill, 1928) are frequently restricted to different (but often related) species or genera of plants. Related species of parasitic insects from the same region also often attack different although related groups of hosts. This occurs in the ichneumonids studied by Mell & Heinrich (1931) and other examples are to be found in the 'Parasite Catalogue' (Thompson 1943-45). In Great Britain, among bees of the genus *Psithyrus*, which infest the nests of bumble-bees, each species is apparently associated with different species of host (Sladen, 1912). The ecological relationships between related species of freshwater mussels (Unionidae) whose glochidia attack fish (Howard & Anson, 1922), and between related species of parasitic Crustacea (Caullery, 1922) and other forms (Pearse, 1939, p. 526) would also well repay careful study. In such an investigation it would be necessary to take every species (and race) in the whole group and to analyse at every stage of the life-cycle both their differences and similarities in ecology (structure, habits) and distribution, and all the factors controlling their population density—physical, intraspecific and interspecific. Investigations of this sort would provide a more accurate knowledge of the nature of the differences between related organisms—e.g. how far they are adaptive—and of the ecological factors involved in the origin of species: a kind of knowledge which Darwin himself sought.

4. SUMMARY

1. Darwin argued from the observation that the potential rate of increase of organisms is greater than that which the resources of the environment can support, that many must perish from the action of the physical environment and of predators, parasites, etc. and from competition. When competition occurs it is severest between organisms with similar needs and habits, and since related organisms, particularly those which have just diverged from the same parent stock, will be most similar in this respect, competition will be severest between them until its own influence causes further divergence. Hence as new forms appear in a given locality, whether by evolving there or by migration after divergence elsewhere, they will either eliminate or be eliminated by their nearest relations unless each diverges so far from the other that competition between them ceases. Then all may survive together, each adapted to its own special habitat. This thesis has been considered by examining examples of competition between different varieties and species under experimental and natural conditions, and the ecology and distribution of related varieties and species in nature.

2. Three kinds of factors are involved in preventing the unlimited increase of an organism: the organism itself (i.e. its' adaptation to the environment), the physical environment and the biological environment. The operation of biological environmental factors is usually density-dependent, while that of physical environmental factors is usually independent of population-density. Except for the very improbable event of a density-independent factor allowing an organism exactly to replace its numbers from generation to generation, only density-dependent factors can permanently control population density.

3. Competition may be defined as the demand at the same time by more than one organism for the same resources of the environment in excess of immediate supply. Only density-dependent factors are directly involved in competition, although density-independent (e.g. physical) factors may, through the competing organisms' own adaptations to environmental conditions, determine its results and also whether it occurs at all.

4. Competition occurs between organisms with similar needs and habits when the ratio of their population to environmental resources reaches a certain value. This ratio may be kept low and competition reduced or prevented by various agencies, e.g. climatic or other physical rigours, predators, parasites, other competitors, a rapid increase in environmental resources, regulation of their rate of reproduction by the organisms themselves, or changes in their nature.

5. If external conditions (other than those brought about by the organisms themselves, for these are part of the process of competition) remain constant enough not to reverse the competitive relationship between them, it can be demonstrated by a simple argument, of which the conclusion seems inescapable, that if two species have *identical* needs and habits they cannot survive together in the same place if they compete for limited resources unless they are exactly balanced in competitive advantage. The same conclusion applies to organisms with *similar* rather than identical ecology, but the necessary degree of similarity can only be discovered empirically. One species may be superior to another either in the combined rate of reproduction and survival independent of interspecific interference, in interference or in numbers. The chance of their being equally balanced is almost infinitely small.

6. Reference is made to work on the population growth of organisms of many kinds from bacteria to man, and competition between different species and varieties is analysed in examples from bacteria, fungi, yeasts, higher plants, Protozoa, planarians, crustaceans, freshwater lamellibranchs, phytophagous and entomophagous insects, mutants of *Drosophila*, fish, amphibians, birds and mammals. In many of the examples neither the factors controlling population density nor the ecological relations between competing species are accurately known; but where these have been investigated the theoretical conclusion described in the previous paragraph proves correct.

7. This principle, that competing organisms with the same needs and habits cannot survive together in the same place, can be used to explain the distribution and abundance of many species in nature and the structure of natural communities (e.g. the relation between the numbers of species and genera). It must also affect speciation. When genetic factors (e.g. polyploidy) initiate breeding barriers and divergence, unless differences in needs and habits arise at the same time, competition between the divergent forms will lead to the elimination of one of them. This seems to have happened in the grass *Spartina*. It seems likely, however, that genetic divergence between two populations consisting of members of the same species is usually preceded by some form of geographical or ecological isolation. Different authors place different emphasis on the roles of these two factors.

8. But whatever the cause of their divergence, related species which occur in the same area will tend to compete if the ratio of population to resources is high enough. It would then be expected that either one will completely eliminate the other from that area or that they will survive together by evolving some form of ecological isolation. In all cases where such species have been studied this proves to be so,

thus fulfilling the conclusion of Darwin's argument. This argument suggests that differences between species and races are usually adaptive, although in special circumstances they may not be.

9. There is need for extensive ecological studies, such as that carried out by Lack on birds, of the

ecology and distribution of whole groups of related species. Investigations of this sort would provide a more accurate knowledge of the nature of the differences between related organisms, and of the ecological factors involved in the origin of species.

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ADDENDUM (see p. 59)

Dr Park has kindly given me permission to mention some results of his large-scale study of competition between *Tribolium confusum* and *T. castaneum* which bear on the subject of this paper. When living alone each species does well in the medium used, but in competition they never survive together in equilibrium. When both species are infected with the protozoan

parasite *Adelina tribolii*, *Tribolium confusum* usually eliminates its rival, although sometimes the reverse occurs. With *Adelina*-free insects, *T. castaneum*, whose single-species populations are the more reduced by this parasite, was more frequently the survivor. These results should be consulted in detail when they are published.