COMPETITION FOR FOOD AND ALLIED PHENOMENA IN SHEEP-BLOWFLY POPULATIONS

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Competition for food among larval populations of sheep blowflies constitutes an important factor limiting the general fly population in nature. Both intra- and interspecific competition take place on carrion. In South Africa the main species of flies concerned are *Lucilia sericata* Mg., *L. cuprina* Wied., *Chrysomyia chloropyga* Wied., *C. albiceps* Wied., and *C. marginalis* Wied.

The degree to which these species suffer loss of population from the effects of intra- and interspecific competition on a carcass is determined mainly by their inherent growth characteristics and by the degree to which they are adapted to withstand the adverse conditions engendered by overcrowding of the larval populations on the available food supply. In this paper the species listed above have been examined on the basis of rigid experimental tests to ascertain their respective responses to competition of varying degrees of intensity. It has become evident that the species of *Lucilia*, which are the most important in relation to strike in sheep, are better adapted than are their competitors to withstand the effects of straightforward competition for food.

Adaptations to meet adverse conditions consist of the rapidity of larval growth and the time at which the most rapid growth period occurs, the ability to form viable pupae at a comparatively low final growth weight and a general reduction in the size of the individuals in a population in favour of an increased total number of survivors. In these respects *Lucilia* spp. are able to achieve greater success than the *Chrysomyia* species. They are therefore always more successful under adverse conditions. An exception is found in the case of *C. albiceps* in which the larvae have predatory habits and are therefore able to destroy competitors on the carcass.

C. albiceps is always characterized by a lower field population than occurs with the other species and is therefore limited in its usefulness as a controlling agent. It is more exposed to the attack of parasites and predators during the vulnerable pupal stage and the general fly population is thereby very considerably reduced during the summer months.

In South Africa, blowflies are seasonal in their appearance on carrion and can be divided into two well-defined groups of summer feeders and winter feeders. These two groups correspond with the classification into secondary and primary blowflies respectively. Overlapping between the two groups occurs at the times when the populations of both are at their lowest ebb. Competition for food is therefore less intense between the primary and secondary groups than it is between species occurring within the same group. Secondary fly populations cannot therefore materially affect those of the primary group.

For this reason and for others which concern its growth characteristics, *Chrysomyia marginalis* cannot appreciably influence populations of *Lucilia* and is therefore not a controlling factor for the latter as has been claimed. When *Lucilia* and *C. chloropyga* occur together on a carcass, the former is always able to survive and to reduce the population of the latter species.

Competition in field populations of blowfly larvae is regulated by a number of factors, some of which have no direct connexion with the fly populations themselves. The quantity of carrion available, for example, is governed by the population dynamics of the animals from which it is derived and by those of the predatory and scavenging groups which prey upon them. During the 20 or 30 years over which the blowfly problem has become more acute in South Africa, it is noteworthy that a considerable change has occurred in the balance between predator and prey populations due to the activity of man. The latter have increased as the former have gradually been destroyed because of their depredations on domestic stock. The amount of carrion, derived from small animals, has therefore increased, providing additional food for blowfly larvae.

From experiments and from field observations it is clear that competition for food can never serve as an efficient controlling factor for blowfly populations. This is especially true for populations of the important primary species (*Lucilia* spp.). Competition acts to produce fluctuations in the populations of flies subjected to it, so that certain years are marked by abnormally large populations of adult flies which produce an increased incidence of strike in sheep. Such years are well known to farmers as 'bad fly seasons'. Reduction of blowfly breeding grounds by means of the destruction of carcasses in the field is not likely to prove efficacious.

It is clear that we require to know a great deal more about the relationships between the populations of flies, their environment, their natural controlling factors and their fluctuations as related to the factors which influence competition in the field before we can hope to evolve any satisfactory measures which are designed as a frontal attack on the blowflies themselves.

I. The nature of the problem

The concept of an all-pervading struggle for existence among organisms in nature holds a prominent place in the tenets of biological science. The form and intensity of this struggle varies from time to time and from place to place with the relevant environmental factors and with the kind of organisms concerned. One of its most striking evidences is in the form of competition for a common food supply between members of the same population of insects, or between two or more different species inhabiting the same environment. It is seen more particularly in insects which rely upon carrion for their means of subsistence.

The source of food for the immature forms of the majority of these species is encountered only on isolated occasions and is usually scattered widely over any given area. The number of available carcasses is limited by the density of the population of the animals from which they are derived and by the mortality factors operating in that population as well as by other events, such as the relative abundance of scavenging animals in the area. Hence, the amount of available food is a significant variable which will fluctuate with time in a manner which is independent of the density of existing blowfly populations.

Each carcass, in itself, represents an essentially restricted environment containing a limited quantity of suitable food. In a warm climate, decomposition proceeds at a fairly rapid rate, and, since each species of fly is attracted to the carcass at a definite stage in this process (see Mackerras 1930), the food supply will remain attractive to a particular species for a comparatively short period. This serves to reduce the *available* food still further.

A situation exists which will tend to produce conditions exceptionally favourable for the incidence of intense competition for food between the progeny of the various species of flies that frequent carrion. If this competition results in the destruction of large numbers of individuals through starvation, or if it results in the production of undersized flies which are deficient in reproductive capacity, then competition, as such, constitutes a valuable part of the complex of mortality factors normally responsible for the limitation of the general fly population. The phenomenon cannot be ignored in any general or detailed study of the natural control of blowflies. Its exact value and its relationships with other natural mortality factors must be assessed as accurately as possible.

The adaptation of what were initially carrion-inhabiting flies to development upon the living animal has never been satisfactorily explained. Wardle(1930) has suggested that the habit was originally induced by the intensity of competition between species for oviposition medium which arises from the nature of the distribution of carrion in the field. On the other hand, the existence of races of *Lucilia sericata* which differ in that the sheep-infesting race possesses the enzyme collagenase which aids in the penetration of intact skins of animals, whereas the other race does not possess this secretion and confines its activities to carrion and necrotic tissues (see Messer & McClellan 1935), may provide the solution to the problem.

With the reason for this change in habit, however, we are not immediately concerned. The fact remains that the flies in question can and do breed very readily on carcasses and must be regarded as primarily carrion-feeders. Hence, the maintenance of their populations in nature will be determined very largely by the availability of carrion. The majority of the flies are produced in large numbers from this source, and a certain proportion of the so-called 'primary flies' will attack the living sheep.

It is thus to the carcass that we should go, first of all, for the fundamental information which is essential as a basis for evolving methods of dealing with the problems involved. We require to know how populations are limited in this environment. It is obvious that a high degree of control must be exerted there if the high biotic potential of the flies is considered. As with all other insect problems, satisfactory methods of control can be devised only when the details of population fluctuations are known.

In spite of the vast array of investigational work which has been published on the blowfly problem throughout the world, this aspect has been comparatively neglected. It is true that a few workers, notably in Australia, have demonstrated that certain aspects of population interactions and their relationship to environmental conditions apparently have an important bearing upon the natural limitation of blowfly populations. These workers have barely touched the fringe of the problem and have remained content with the demonstration of the presence or absence of factors. More extended treatment is essential if we are to derive any substantial benefit from the knowledge gained.

For example, the bare statement that competition for food constitutes a main factor in control is not sufficient. Few practical conclusions of value can be drawn from it. It is not enough to have a *general* picture of what happens. We must know *exactly* how competition works, its quantitative relationships and the extent to which it is responsible for the reduction of a given fly population under given conditions. It is then possible to evaluate its importance in true perspective and to consider its exact place in the economy of the fly. In the absence of such data, some very premature and rash conclusions have been deduced.

It is comparatively rarely that insect populations are limited almost entirely by the available food supply under natural conditions. In the case of the vast majority of phytophagous insects, an abundance of food material usually exists in the environment, and only in the event of exceptionally heavy outbreaks of the insect (which occur sporadically, usually at intervals of several years, and which may be traced to the temporary failure of some other natural check to increase) will there be anything approaching competition for food among the individuals in the population. Such competition may be found among pests of stored products, but it is in the case of the carrion-infesting Diptera that the phenomenon constitutes a normal feature in the population. For this reason, they provide excellent material for the study of this aspect of population dynamics.

Competition and allied phenomena can be produced and controlled very easily under experimental conditions without seriously affecting the normal environmental conditions of the insects concerned. They can therefore be studied in detail in the laboratory. It was from this point of view, as well as from the importance of the practical problems involved in blowfly control, that the present series of investigations were carried out. They form an essential part of a more extensive programme of work on the natural control of the flies which is in progress at the Parasite Laboratory, Pretoria.

II. Review of the literature

In 1894, Mégnin published an account of his observations on the fauna of human corpses and presented a system for calculating the age of a dead body by means of the insects present at the time of examination. This is the first published account of an attempt to deal with ecological succession in carrion. Mégnin recognized eight stages in the decomposition of a corpse, and his paper lists a large number of species associated with these stages.

More recently, De Stefani (1921) again emphasized this association and pointed out the practical value of the phenomenon in medico-legal practice. His paper dealt with the particular insects appearing during each stage of decomposition and discussed their respective roles in the reduction of the dead body. A year later, Fabre (1922) also published an account of succession in carrion.

During each stage of decomposition, there is normally a certain degree of competition for the available food supply between the insects developing on the cadaver. There is also an overlapping between the different populations in the successive stages which has the effect of accentuating the results of competition on each preceding species. The competition for a common food supply, and for one, moreover, of an essentially limited nature, is an important factor in the limitation of the populations which can develop to maturity.

This was demonstrated by Holdaway (1930) in a summary of his conclusions derived from a quantitative study of insect populations on carrion made in the south of France. This author was primarily interested in the blowfly problem. His observations extended from the beginning of putrefaction to the disappearance of all the consumable parts of a carcass. Holdaway pointed out that the greatest factor concerned in the reduction of the fly populations on carrion is dipterous competition and its associated predatorism.

Lucilia sericata is the first member of the ecological succession and is subject to severe intraspecific competition during the larval stage. Subsequent species of Diptera in the succession contribute to accentuate this competition and ultimately to reduce the population of *Lucilia*. The greatest reduction found was that produced by the larvae of Sacophagids and the semi-carnivorous larvae of *Chrysomyia*. Thus a bait containing approximately 1 kg. of consumable meat and exposed during midsummer, had an initial population of about 50,000 *Lucilia* larvae, whereas the final emergence was 231 flies.

In a further experiment with the same quantity of bait, initial populations of approximately 60,350 *Lucilia sericata* and 2850 *L. caesar* gave rise to a final *Lucilia* population of only thirty flies. In this case, *Chrysomyia* was largely responsible for the drastic reduction, the final population of this species being 2611 flies.

Mackerras (1930) pointed out that there is experimental evidence to show that a given species of insect is only able to thrive on carrion during a certain stage of decomposition. Furthermore, there is evidence to show that the progress of this decomposition is profoundly influenced by the insect inhabitants. For example, the particular type of liquefaction which is suitable for the development of *Chrysomyia* normally does not supervene unless *Lucilia* larvae are present. Thus, the environment of the larvae of a particular species of blowfly can no longer be considered as *any* carcass, but only those carcasses in a particular stage of decomposition.

The same author also emphasized the great importance of the intense competition for food and space among blowfly larvae and the effect of the rapid succession of species on this competition. It was concluded that the amount of food available for the larvae is the primary factor limiting the abundance of blowflies. Any factor which tends to reduce the severity of competition, as, for example, natural enemies of the blowflies, is inimical to control. Up to a point, reduction in the population density increases the efficiency of the flies, since the less intense the competition, the larger and more vigorous and fertile are the emerging flies.

Intraspecific competition among experimental populations of *L. sericata* was also described by Salt (1930), who recorded that the high reproductive rate of this fly was largely neutralized by the habit of laying more eggs on a carcass than the latter can support. He noted that, when increasing numbers of eggs of the same age were placed on equal portions of meat, the size of the adults became gradually smaller, the mortality during the larval period increased and, beyond a certain point, fewer adults were obtained than the amount of food was capable of producing.

In a later paper, Salt (1932) suggested that since the numbers of *L. sericata* are very largely kept in check by competition among larvae in the presence of a dearth of food, other dipterous larvae which are competitors should be considered of importance in control. If it could be proved that *Lucilia* is the original colonizer on living sheep, it might be useful to protect these other competing species. This author expressed the opinion that the reproductive rate of *Lucilia* is such that biological control methods are impracticable.

Wardle (1930) listed the unfavourable ratio between the female-fly population density and the available mass of oviposition media as one of the main significant variables in the blowfly environment which limit potential abundance. Competition is induced between ovipositing females which restricts the potential egg production and induces an unfavourable ratio between the number of eggs deposited per unit mass of medium and the number of larvae which can secure feeding positions within the medium.

A more detailed account of ecological succession and competition in carcasses was given by Fuller (1934). In this paper, a list is given of the insects associated with carrion in Australia, together with notes on the principal species of Diptera, Coleoptera and Hymenoptera. The seasonal abundance and distribution of blowflies are dealt with as a preliminary to a discussion of succession and competition. The main conclusion reached by this author is that competition for food and space between blowfly larvae in a carcass constitutes the main factor regulating the general blowfly population, i.e. that the population of emerging adults is primarily determined by the amount of food available to the larvae.

Fuller pointed out that the proportion of a primary species in the total population of flies is determined by a number of factors, such as intraspecific competition, which reduces the size and number of individuals; competition with other primary flies, which intensifies the effect of intraspecific competition; and competition with secondary flies and the attack of predators, which reduce the numbers without affecting the size.

The effects of competition are seen in an increase in the total mortality in the population of larvae and in the decrease in size of the resulting flies as well as in their fecundity. Thus, Herms (1907) observed that *L. caesar* attained a size which was directly proportional to the number of feeding hours and hence to the amount of food obtained by the larvae.

Smirnov & Zhelochovtsev (1926) tested the effect of cutting off or reducing the food supply of larvae of *Calliphora erythrocephala*. They found that a differential effect was produced in the size of different regions of the wings when the total size of the fly was reduced by this means after a given time.

Herms (1928) found that the size of adults of *L. sericata*, as measured by the length of the wing, became increasingly larger as the larval feeding period was increased. He also stated that the sex ratio was reversed from a large preponderance of females in the normally fed populations to a preponderance of males in the underfed. He concluded from this that, for certain flies at least, the larval females require a larger amount of nourishment than do the males. His data on the latter point, however, are not convincing, being drawn from small samples showing a wide variation. Where larger samples were taken (e.g. 100 or more individuals) the sex ratio would appear to be approximately 1:1 in both cases. Later workers have found that there is no effect on the sex ratio which can be traced to under-nourishment. Weidling (1928) made deductions similar to those of Herms when working with *Calliphora erythrocephala*, but his data are open to the same objections. He suggested that there may be a heavier mortality in the females due to starvation in the larval stage.

According to Mackerras (1933), the number of eggs which can be laid by a fly at any one time is dependent upon its size and thus upon the amount of food it obtained during the larval stage. Starvation at this time did not have a marked effect upon the sex ratio which, in *Lucilia*, is close to 1:1.

The effect of competition for food among the larvae of the carrion fly, *Phormia groenlandica*, is reflected in a decrease in weight of the individual pupae as well as in a reduction in the number of flies produced (Smirnov & Vladimirova 1934). In a series in which the number of larvae on a standard-sized piece of beef liver was varied from 25 to 2000, the 'biomass', calculated when the pupae were 1 day old, was expressed as the total weight of all pupae obtained in each experiment and was represented by a curve. The weight of the pupae first increased with an increase in the original number of larvae used to a maximum when the number was 600. It then dropped, at first rather sharply and then more gradually, to a minimum when the initial number of larvae was 2000.

Working with small carcasses of varying sizes, kinds and weights, Fuller (1934) recorded that, as the number of maggots on the carcass increased, so did the length and weight of the resulting puparia decrease. Flies arising from overcrowded carcasses were much smaller than normal flies and were less prolific. The number of flies emerging from a carcass is not always a reliable figure, according to this author, as there is often a heavy pupal mortality under artificial conditions which is due to unknown causes and is not related to competition at all.

Fuller also found that the sex ratio was not affected by larval overcrowding. Before a reduction in numbers occurs, it is preceded by a reduction in size of the individuals to a minimum. With increasing intensity of competition, there is less food for each individual maggot and the tendency is for most to survive, although semi-starved and unable to attain their full size. The size of the pupating maggots decreases to a minimum with overcrowding of a certain intensity, and the resulting puparia and flies are very under-sized, often abnormal, and the flies less prolific than usual. Mortality in the larval stage also increases with intensity of competition.

In interspecific competition between different species of primary flies the results, according to Fuller, are similar to those of intraspecific competition in that it operates to limit the size of the pupating maggots and hence that of the puparia and flies and does not produce a high larval mortality. The maggots of *Chrysomyia* attack and eat those of the primary flies and so relieve overcrowding among the latter. Any predator must lessen competition if it attacks the larvae sufficiently early. Fuller considered that competition between primary flies therefore results in large numbers of under-sized adults; while, when *Chrysomyia* is present, the adults emerging are fewer and larger.

In South Africa, Hepburn (1943) recorded preliminary results of the investigation of succession and competition in carrion. The phenomenon had already been noticed by Smit (1931). Beyond a difference in the species present, these accounts do not add anything to our general knowledge of the subject beyond that outlined above, since they deal exclusively with the end-results of carcass exposures.

In summarizing the work done on insects which frequent carrion, we find that

(1) there is an ecological succession of insect species on carcasses;

(2) this can be correlated with changes which take place during the decomposition of the cadaver;

(3) the stages in this succession frequently overlap to a considerable degree, especially in hot climates;

(4) both intra- and interspecific competition for food and space occur on the carcass between larval forms of dipterous insects;

(5) this competition constitutes one of the main factors which control or limit the density of the resultant fly population;

(6) competition also reduces the size and fecundity of the flies as well as increasing the total mortality during the immature stages;

(7) some species in the succession are predatory in habit as well as feeding upon the carrion, and these species tend to reduce competition in other flies present as well as reducing the populations directly, so that fewer but larger flies tend to be produced.

As a footnote to this summary, the observation of Mackerras (1930) may be added. He notes that despite the heavy mortality during the larval stage, there still remain more blowflies than would be sufficient to fill the available larval environment.

Obviously, although competition for food appears to be such a potent factor in reducing fly populations, it is still not efficient enough to provide an adequate control over them. It seemed worth while, therefore, to make a more extensive investigation of this factor and its relationships to other control factors than has been done hitherto.

The above represents a general outline of the information available from the literature. Unfortunately, it is devoid of any exact treatment of the subject. The most detailed work, that of Fuller mentioned above, does not give enough systematically accumulated data on which to base further work on the biotic complex of carrion. The South African records are totally inadequate.

III. Materials and general methods

1. *The species used*

The present investigations have been confined to the relationships of the main species of flies which are associated in the complex of insects which breed on carrion in South Africa. These are *L. sericata* Mg., *C. chloropyga* Wied., *C. albiceps* Wied., and *C. marginalis* Wied.

According to Smit (1931), the main primary fly is *L. sericata*. This is followed in importance, and also in its time of attack on living sheep, by *C. chloropyga*. On the other hand, *C. albiceps* is a secondary fly which oviposits on sheep only after primary maggots have become established. It is possible that, in a great many cases, *C. chloropyga* also follows *Lucilia* in strikes and therefore acts on these occasions as a secondary fly. *C. marginalis* is not a sheep blowfly but occurs commonly on carrion.

All of these species breed very readily and in large numbers on carrion, which undoubtedly forms the source of the main bulk of the fly populations in the field. In warmer weather, oviposition by these species takes place on a carcass in a definite sequence. That by *Lucilia* occurs first while the carcass is comparatively fresh. It is followed at intervals of an hour or less by *C. chloropyga* and *C. albiceps*.

It may be objected, on the grounds of assertions by recent workers on the blowfly problem (Hepburn 1943 *a*, Mönnig & Cilliers 1945), that primary strikes in sheep are, in the great majority of cases, to be ascribed to *L. cuprina* Wied., and that this species should have been used in the present investigations in preference to *L. sericata*. The present writer (Ullyett 1945) has shown that the two species of *Lucilia* interbreed very readily and that the main character which has been used for the separation of field material, namely the green femur of the foreleg of *L. cuprina*, behaves as a Mendelian dominant with tetraploid characteristics. This character is inherited by the F_1 generation of progeny from the cross and segregates out normally and in a well-defined manner in the F_2 generation, so that, although it appears in five-sixths of the population, only one-sixth is the pure form of *L. cuprina*, the remainder being hybrids. This character is not a valid means of specific identification, and its acceptance as such has undoubtedly led to much confusion. It is suggested that *L. cuprina* is merely a form of *L. sericata* and, until a much closer examination of the extensive series of material obtained from sheep can be made, it must be assumed that a large proportion of the records dealing with *L. cuprina* from the living animal refer, in reality, to the hybrid form. On this basis, the status of *L. sericata* as a sheep blowfly must be restored.

In an examination of the larval forms of *L. cuprina* and *L. sericata* obtained from pure strains, no morphological difference could be found which was sufficiently important to warrant specific separation. Furthermore, *L. cuprina* and *L. sericata* are biologically identical, and no difference in habits or development was observed when they were reared on meat in the insectary. This supports the conclusions drawn from the genetical studies described above.

For these reasons, it would seem that either form could be used in experimental work such as will be described below without affecting the general application of the results obtained. In the present work, the form known as typical *L. sericata* was used throughout.

The third species of *Chrysomyia*, namely, *C. marginalis*, is not a sheep blowfly, although it is known to cause myiasis in other animals and is therefore to be regarded as a pest species. Since it occurs on carcasses and thereby enters into competition with other insects found thereon, it is intimately bound up with the blowfly complex and must be considered in that connexion. This is the more important in view of the role which has, rather prematurely, been assigned to it by South African workers. Unfortunately, this fly is somewhat difficult to rear in captivity, and it has not been possible to obtain any regular oviposition giving sufficient material to conduct experiments comparable with those carried out with the other species of Diptera. The information which is available relating to *C. marginalis* will be dealt with separately.

2. *Treatment of larvae and pupae*

All three species of blowflies oviposit and develop very easily on fresh meat. Laboratory rearing of larvae was carried out on meat of a standard quality. Preliminary tests were made of a number of different media. Some of those used by other workers, such as minced beef, ox liver and fish offal, were found unsuitable for one reason or another. The use of small animal carcasses was also out of the question owing to the impossibility of standardizing the quantity and quality of available food.

Solid pieces of fresh, lean beef were found to be most suitable, provided they contained a minimum of fat and sinew. The size of the piece used for cultures was standardized. Too small a piece tended to dry out too rapidly, while a piece which was too large made it impossible to count out sufficient larvae within the given time in order to give the more extreme conditions of overcrowding. After tests, it was found that the minimum size compatible with the desiderata was a piece measuring approximately 3 in. square by 1 in. thick and weighing exactly 140 g. This was adopted as the standard meat ration throughout the investigations.

The meat was placed in a shallow pan of galvanized iron of a standard size. After the larvae had been counted on to the meat, the pan was placed over a layer of sifted sand in the bottom of a breeding box. The latter was fitted with a gauze-covered lid, fine-mesh copper wire gauze being used for the purpose. This, together with similarly protected holes in the sides of the box, provided ventilation while at the same time preventing the access of parasites and predators. A considerable amount of gas is generated during the decomposition of the meat, particularly ammonia, and good ventilation of the boxes is essential. The overall dimensions of the box were 18 in. square by 4 in. deep.

The boxes containing the cultures were kept in a breeding chamber at a constant temperature and high relative humidity until the larvae pupated. The sand was then sifted and all puparia removed from it and from the meat pans. The puparia were counted and measured on the same day and were afterwards placed in 1 lb. honey jars or in quart Mason jars until the flies emerged. The mouth of the jar was closed with a screw top having ventilation holes covered with the fine-mesh copper gauze. Exposure of puparia on work benches and elsewhere was always kept as brief as possible in order to minimize the chance of parasitism by *Mormoniella vitripennis* Walk., a parasite which is usually present in the neighbourhood and which very quickly finds and oviposits in exposed puparia.

3. *Oviposition*

Stock flies were kept in large cages, covered with 24-mesh wire gauze, in a small insectary building where abundance of light and ventilation were obtained by making the whole of one side of the building, at the level of the cages, to open upwards. Normally kept open during the daytime, this side was closed during the night and in inclement weather. The insectary was fitted with electrical tubular heaters with thermostatic control whereby the temperature could be raised during cold weather. No attempt was made to keep it constant.

When eggs were required, shallow pans with meat were placed in the cages during the morning and were examined every half-hour for eggs when these were needed for experimental purposes. In addition to the meat meal which the flies obtained on these occasions, sugar, raisins and water were supplied at all times. Clean sand in trays was saturated with water, this method serving to prevent accidental drowning of flies. During very hot and dry weather, cages were sprayed with water at intervals in order to raise the humidity.

The importance of sunlight in the successful treatment of adult flies must be emphasized. With an inadequate supply of daylight, mating was secured only with difficulty and the oviposition was very irregular. In the case of *C. albiceps*, direct sunlight was necessary to secure reproductive activities.

4. *Experimental technique*

In all experiments on the effect of competition for food among blowfly larvae, eggs were allowed to hatch overnight on the meat on which they were deposited. The young larvae were counted on to the standard piece of meat in the numbers required. Removal of larvae was most easily effected by means of a wet camel-hair brush. The aim throughout the experimental series was to obtain satisfactory statistical data. With this in view, at least six replications of each separate treatment were carried out. This was generally found to be sufficient.

All experimental work, except where otherwise stated, was done at a constant temperature of 80° F in the breeding chamber. In the case of the larval cultures, a high relative humidity of approximately 80% was maintained in the room in order to prevent the premature desiccation of the meat. Absolute cleanliness in the breeding chamber and in the breeding boxes was essential in order to prevent disease attacking the cultures.

As far as possible, the same staff was kept on the mechanical routine of counting, measuring and weighing. Unavoidable staff changes tended to the introduction of a certain amount of variability due to personal error. This was particularly so in the case of measurements, but, on the whole, was so slight as not to affect the general utility of the results to any extent. All measurements were done with vernier callipers and all weighings on the same, air-damped chemical balance which was correct to 0·01 mg.

Routine work was strictly supervised and any series which developed abnormal symptoms or which showed obvious faults in technique and errors of judgement were summarily rejected. The work was done very largely by technical assistants who were specially trained to give accurate service. Without the help of these assistants,t he work of accumulating the necessary data would not have proved possible.

IV. Normal larval growth

1. *Method*

The progress made in the normal growth of individuals in a population of larvae, i.e. growth made when optimum conditions prevail and no shortage of food occurs, was determined by taking random samples of the population and by measuring the increments in growth weight at known intervals of time. Weighings were continued until the larvae commenced to pupate. The same number of individuals was taken in all samples, and the larval growth weight of each species concerned was expressed in the form of the weight increments of 100 larvae.

Overcrowding of larvae on the meat and the consequent shortage of food was avoided by adjusting the initial larval population so that it should not exceed approximately 200 individuals on the standard piece of meat (140 g.). All cultures were kept at 80° F, and a high relative humidity was maintained.

Larval samples were weighed at the stated times (figure 1 et seq.) as rapidly as possible. Weights were taken to four places of decimals. Before weighing, the fluid which normally surrounds the larvae in the meat and which tends to adhere to them when they are removed, was absorbed by blotting paper on which the larvae were gently rolled. This fluid is composed mainly of predigested protein material, digestive secretions and larval excreta as well as some moisture from the meat itself. It forms an appreciable source of error in weighing unless removed.

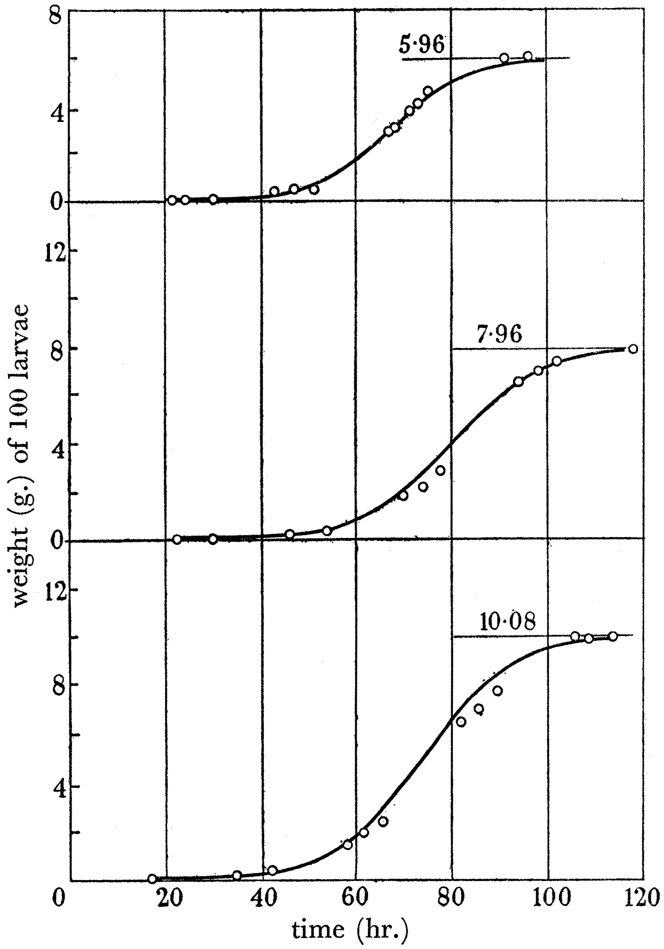

Figure 1. *L. sericata.*

$$y=\frac{5{\cdot}96}{1+e^{8{\cdot}74988-0{\cdot}1308t}}\,.$$

Figure 2. *C. chloropyga.*

$$y=\frac{7{\cdot}96}{1+e^{8{\cdot}52-0{\cdot}107t}}\,.$$

Figure 3. *C. albiceps.*

$$y=\frac{10{\cdot}08}{1+e^{7{\cdot}83-0{\cdot}106t}}\,.$$

Figures 1 to 3. Normal growth of blowfly larvae on lean beef.

Eggs deposited by females during the daytime hatch out during the following night, the incubation period being approximately 12 to 16 hr. according to the species and temperature. For this reason, eggs were placed on the meat when laid and any excess larvae were removed the next morning. The curves depicting growth have their origin at the time when eggs were laid and are thus representative of both incubation and larval periods. The times taken for oviposition are correct to within 30 min. As an additional precaution, meat was added when the original ration was drying out or was becoming exhausted towards the end of the feeding period.

When fully grown, larvae crawled off the meat or remained to pupate in or under the remains of the medium according to the habit of the species concerned.* Puparia were measured in order to provide a final check upon the maximum growth weights attained. In

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* There is a marked difference between the three species of flies as regards pupation habit. This will be discussed in a future communication.

all cases, the mean pupal lengths obtained showed that the conditions provided were optimum for full development of the larvae.

Loss of weight occurs immediately prior to each ecdysis and also just before pupation, notably when fully grown larvae are crawling off the meat. This loss was taken into consideration when making weighings. It was a useful indication to the maximum growth weight during the last few weighings.

2. *Results*

The normal growth of *L. sericata* larvae is shown in figure 1. The maximum growth weight was 5·96 g. per 100 larvae. The time taken to reach this was approximately 91 hr. from the time of oviposition. The most rapid larval growth took place between 50 and 80 hr. from egg-laying.

Under similar conditions, the larvae of *C. chloropyga* reached their maximum growth point in 118 hr., the weight of 100 larvae being then 7·96 g. (figure 2). The larvae grew most rapidly during the period between 60 and 90 hr. after oviposition.

C. albiceps attained the peak of its growth at 109 hr., the asymptotic maximum being 10·08 g. per 100 larvae (figure 3). The period of most rapid growth was between 64 and 96 hr.

The growth of 100 larvae of each of the three species, in pure culture and under optimum conditions, may be compared as in Table 1.

TABLE 1. SIGNIFICANT DATA FOR NORMAL LARVAL GROWTH

species	maximum growth weight (g.)	time attained (hr.)	period of most rapid growth (hr.)	increment per 100 larvae per hr. (g.)
L. sericata	5·96	91	50–80	0·0648
C. chloropyga	7·96	118	60–90	0·0675
C. albiceps	10·08	109	64–96	0·0925

3. *Discussion*

The above data give clues to the probable success of the three species when growing under conditions of intraspecific competition for a limited mass of food. Although other factors may come into play as the larval population in the medium is increased, the characteristic phenomena of growth must play a major part in determining the size of both the population and the individuals which can be produced on the available food. The three species differ fundamentally in their manner of growth, and they may be expected to differ in their response to variations in the food supply.

Of the three species, *L. sericata* attains to the smallest maximum growth weight. The food requirements of the larvae will be roughly in proportion to their weight when fully grown. A piece of meat of a given size and weight will therefore be able to support more larvae of *Lucilia* to maturity than of the two remaining species. Assuming that a larva requires at least as much food by weight as is equivalent to its own weight at maturity, then 140 g. of meat, if it is all consumable by the larvae, should be sufficient for the needs of approximately 2349 *Lucilia* larvae, or 1389 larvae of *C. albiceps*, or 1759 larvae of *C. chloropyga*. It is clear that a very much larger population of *Lucilia* can occupy a given carcass without encountering shortage of food and the concomitant intraspecific competition than is the case with the Chrysomyias. In this respect, *C. albiceps* is the least favoured species.

In the rapidity with which the maximum growth weight is attained, *Lucilia* again scores an advantage over the two species of *Chrysomyia*. In nature this is important, since the shorter the development period, the less chance do the larvae run of becoming affected by adverse factors such as natural enemies, changes in physical conditions in the environment (e.g. weather) and deterioration of the food supply. In addition, the more rapidly developing species is the more likely to escape the worst effects of competition for the available food supply, both with co-existing species and with later arrivals. In these respects, *Lucilia* is superior to *C. chloropyga*.

During one period of development, the larvae of all species grow very rapidly for approximately 30 hr. During this time the assimilation of food proceeds apace. The actual time when this occurs differs in the three species. In *Lucilia* it commences about 10 hr. earlier than in the Chrysomyias. This is clearly an important period in the life of the maggot, and any shortage of food during this time will produce the greatest effect upon the size of the fully grown larva. Here, again, the capacity for the utilization of the available medium in the shortest possible time confers a distinct advantage on *Lucilia* in the struggle for existence. The sooner this period of rapid growth occurs in the life of the larva, the more likely is it to happen before any shortage of food arises.

Notwithstanding the above, *Lucilia* does not increase in actual weight more rapidly than the Chrysomyias if the weight increments per unit of time over the whole growing period are taken as the measure. *C. albiceps* has a greater increment while *C. chloropyga* is approximately the same as *Lucilia*.

From an examination of growth characteristics, it would appear that *L. sericata* has very distinct advantages when compared with the two *Chrysomyia* species. From this aspect alone, it would be expected that populations of *Lucilia* would prove more successful under the more stringent conditions in the field. Since other factors serve to modify populations in nature, however, a discussion of the relative success or efficiency of the species must be deferred until more extensive data have been presented.

V. Intraspecific competition

1. *Effect on larval growth*

By gradually increasing the number of larvae which are placed initially on to a piece of meat of standard size, a point is reached at which overcrowding of the medium takes place and there is insufficient available food (i.e. food that can be consumed by the larvae) to support all the individuals to normal, fully grown larvae. Competition for the consumable portion of the meat takes place in the population. Consequently, as all the larvae presumably start life with approximately equal chances of development and survival, none of them is able to obtain its full requirements. This happens, for example, when 2000 *Lucilia* maggots occupy the same piece of meat (140 g.). The position is even more pronounced with a like number of *Chrysomyia* larvae, since they are heavier than *Lucilia* and need more food per individual.

Cultures of 2000 larvae of *Lucilia* and of *C. albiceps* respectively on standard pieces of meat were kept under conditions as before and compared with control cultures, in which overcrowding did not occur. Sample batches of maggots were weighed at intervals throughout development. The results are shown in figures 4 and 5. In both species, a deficiency of food neither shortened nor lengthened the total growing period of the larvae. Two marked effects of the overcrowding were:

(1) a general slowing up of the growth increments during the period of most rapid growth,

(2) a marked decrease in the final growth weight.

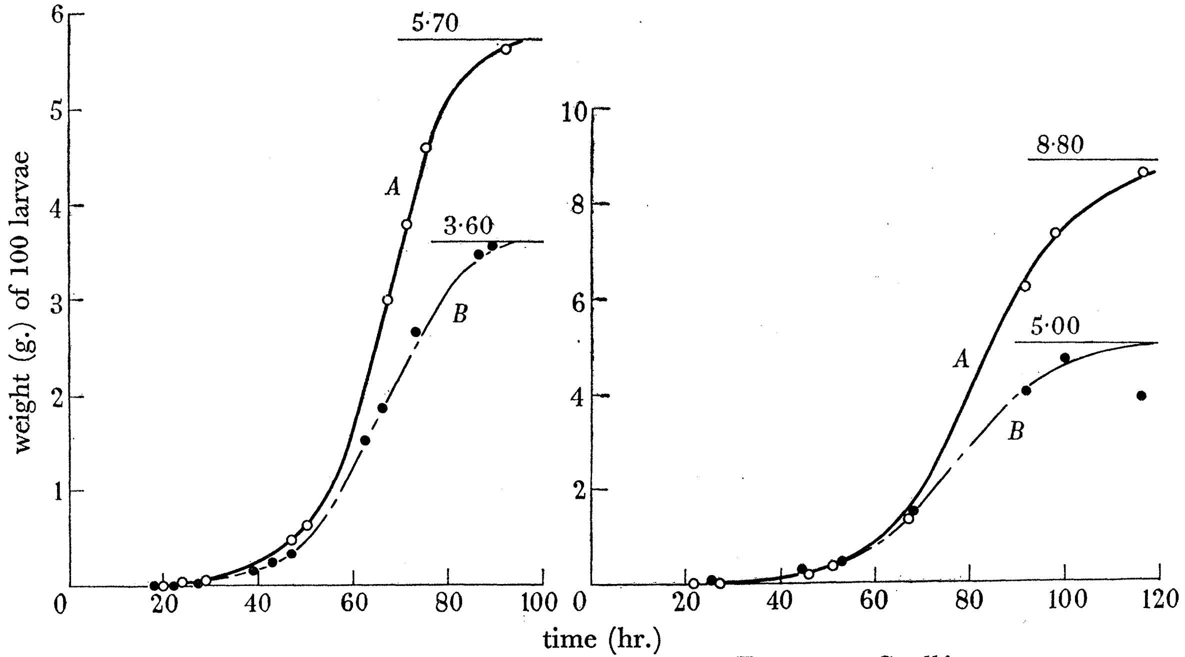


Figure 4. *L. sericata.* **Figure 5.** *C. albiceps.*

Figures 4 and 5. Effect of intraspecific competition for food on larval growth.

In the first instance, competition for the inadequate food supply caused a decrease in the amount which could be assimilated per larva per unit period of time. The final effect was to produce a fully grown larva which was subnormal in size and weight and which gave rise to a small pupa and, later, to an under-sized adult.

During this experiment, no record of mortality was made. That mortality does occur and that competition for food increases it by promoting death of the less successful and robust individuals in the population by direct starvation, is certain. As will be seen later, this happens in a definite manner. Competition has a drastic effect on the total weight of blowfly material produced by a given quantity of food and, if it is severe enough, may cause this production to fall far short of the potential represented by the quantity of meat available.

Earlier in this paper, it was estimated that approximately 2349 fully grown *Lucilia* larvae of maximum size and weight could be reared on 140 g. of meat if all of it is consumable by the maggots. Yet, where only 2000 were placed on the meat, the final weight of the larvae was much below the maximum. It is obvious that the assumption which was made regarding the availability of the meat was incorrect. An appreciable percentage of it was clearly of no value to the larvae as food. An approximate estimate of the unconsumable portion will be made later.

2. *Effect on pupal size*

As a measure of the effect of competition for food on the production of pupae, Russian workers and others have used the so-called 'biomass', or total weight of all pupae formed. This method of assessment is open to two objections:

(1) the rapid loss in weight which takes place in the pupae from the time of formation of the puparium until the emergence of the fly, and

(2) the extremely irregular manner in which pupation of the individuals comprising the population takes place.

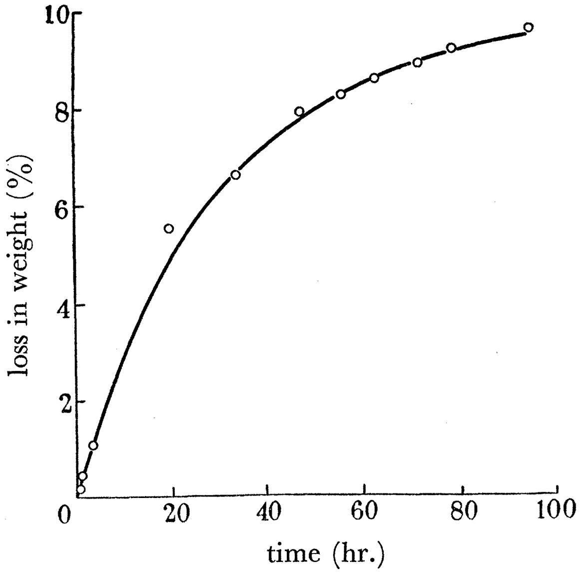


FIGURE 6. *L. sericata*: progressive loss in weight of puparia. $y = 10{\cdot}0(1 - e^{-0{\cdot}0322x})$.

Although it might be possible to ensure that all pupae are weighed at the same stage of development, the second objection makes it impossible to do this on any but a very small scale. The labour and time involved would be too great on the scale used in the present investigations. In addition, the rate of loss in weight of pupae depends upon the saturation deficiency of the atmosphere and, unless the puparia are to be kept under conditions where this does not vary, any changes in atmospheric humidity would immediately introduce an error into the weights.

This is illustrated by the curve showing the progressive percentage loss in weight in the case of *Lucilia* pupae (figure 6). These were kept in an atmosphere having a constant saturation deficiency of 7 mm. mercury and a constant temperature of 80° F for 4 days. Even during the first 24 hr. a considerable and somewhat rapid loss takes place. The rate of loss tends to slow up towards the end of the period, i.e. as the time for the emergence of flies approaches.

Because of this rapid decrease in weight, it was decided to adopt the length of the puparium as a measure of the effect of competition on the size of the resulting population. This was satisfactorily stable throughout if it was taken when the puparia had hardened properly. It served to give a reliable indication of the size of the larva from which each pupa had developed as well as of the size of the adult fly which emerged later.

A definite relationship exists between size and weight, and it is a simple matter to translate one into terms of the other if so desired. In the case of each species, pupae were selected which had all been formed at the same time and were sorted into groups according to their puparial lengths. Each group was then weighed separately and the weight plotted against the mean length for the group. Curves were obtained (figures 7 to 9) from which the weight of a pupa can be determined from its relative length.

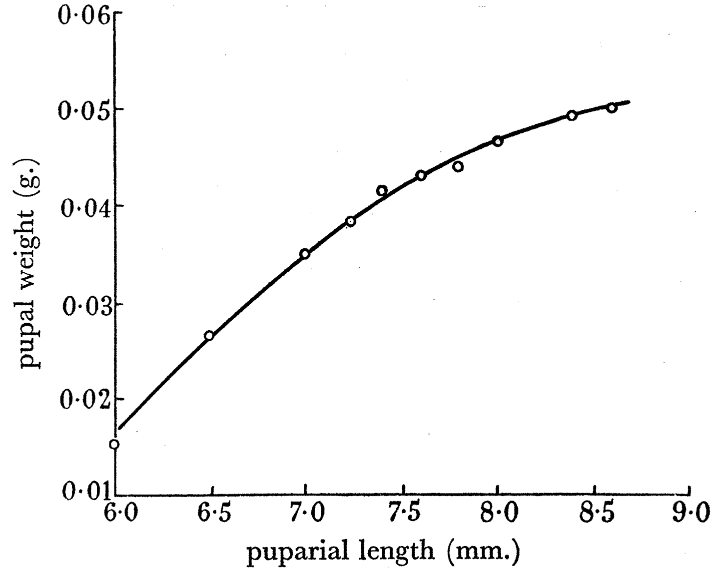


FIGURE 7. *L. sericata*: relationship between puparial length and weight. $y = \dfrac{0\cdot0530}{1 + e^{9\cdot25645 - 1\cdot41226x}}$.

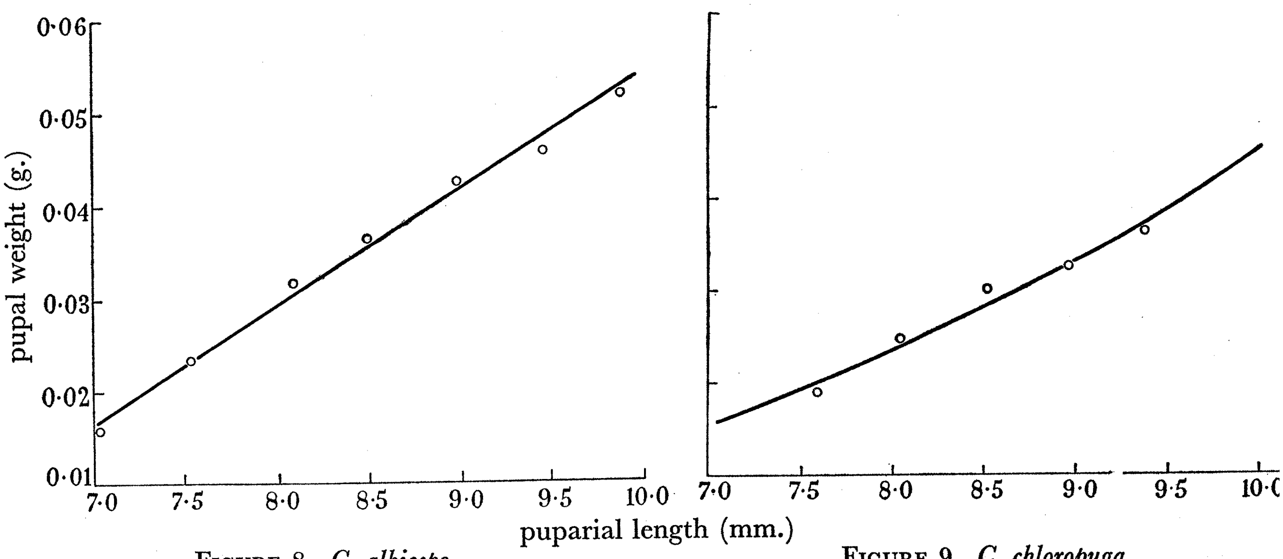


FIGURE 8. *C. albiceps.* FIGURE 9. *C. chloropyga.*

FIGURES 8 AND 9. Relationship between puparial length and weight.

To obtain a range of conditions which would give different degrees of competition for food, a series of cultures was made on which different initial numbers of larvae were placed. The series commenced with 100 newly hatched larvae per 140 g. of meat, in which no overcrowding occurred and continued with groups in which 500, 1000, 2000, 3000 and so on up to 16,000 larvae were used on the standard meat ration. There were six replications of each culture. All of the pupae formed in each replication were counted and a random sample of 100 was used for measurement. From the measurements of length in the samples of the six replications in each series, a frequency distribution was drawn up and a mean value for puparial length obtained. Cultures in which less than 100 larvae survived to pupate were not included, the mean lengths in each case being used in the general summaries of results only.

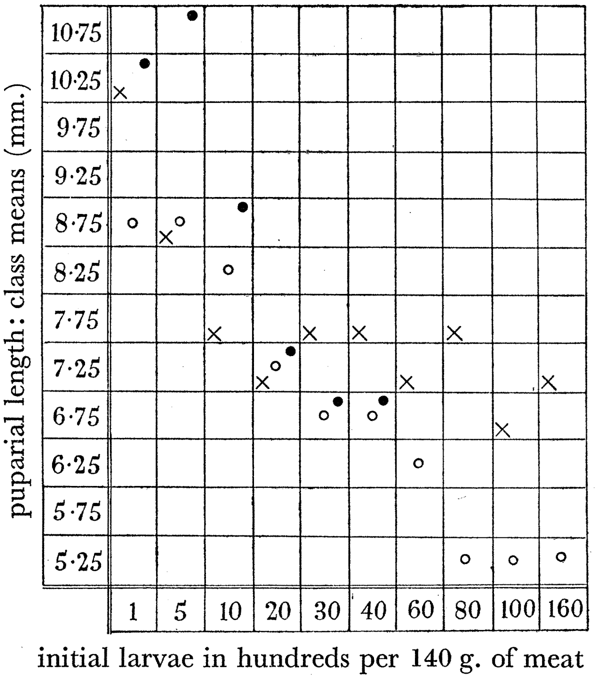


FIGURE 10. Intraspecific competition: shift in modal size group of puparia with increasing initial larval density. ○, *L. sericata*; ●, *C. chloropyga*; ×, *C. albiceps*.

In all three species, the modal length decreases more or less rapidly with increasing degrees of overcrowding (figure 10). This decrease continues until a point is reached at which a large proportion of the pupae approach the absolute minimum size for the species. Larvae which have not developed up to this standard do not produce pupae but die. This minimum level differs with the species concerned, as does the difference between the absolute maximum and minimum sizes attained. Thus *Lucilia* can produce a smaller viable pupa than can either of the Chrysomyias because of its smaller larva, but the difference between the mean maximum and minimum puparial lengths is less than in *C. chloropyga* and greater than in *C. albiceps*.

The size of the pupa is dependent upon the amount of food which is absorbed during the larval stage. Competition for food, by reducing the amount that can be used by the larva within a given period, causes a corresponding reduction in its ultimate size. It may be assumed, for the moment, that the material contained in a standard ration of meat is all available for consumption, and that it becomes divided up equally between the individuals in the population present on it. If the puparial size is plotted against the weight of meat available to each larva, a curve is obtained which depicts the relative growth in size with the increasing food supply. This has been done for each species separately (figures 11 to 13). A definite general relationship is shown which puts in a more concrete form the general observations of previous workers. The actual form of the curve differs with the species concerned.

It is not possible to compare the absolute puparial lengths of the three species since the relation between length and weight varies with the shape assumed by the puparium. There is therefore a marked difference, as between species, in the relationship of length to breadth and mass. *C. albiceps*, for example, has the heaviest mature larva which presumably requires the largest amount of food and which produces a puparium of 10·1 mm. in length under optimum conditions. On the other hand, *C. chloropyga* has a larva which is considerably lighter but which gives a puparium which is somewhat longer (10·8 mm.).

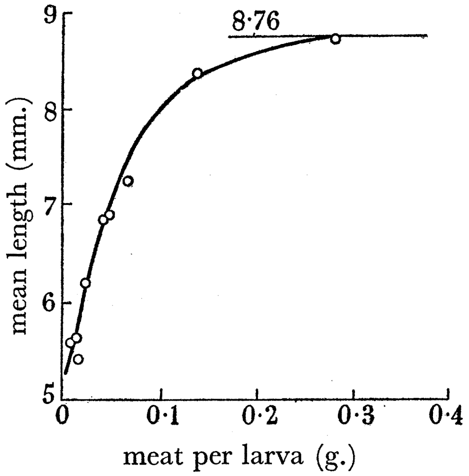
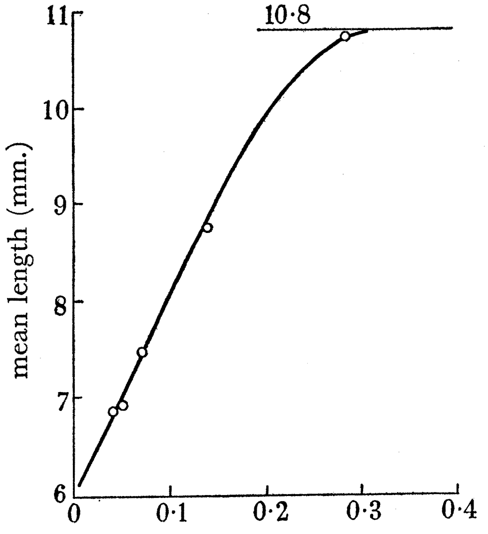


FIGURE 11. *L. sericata.*



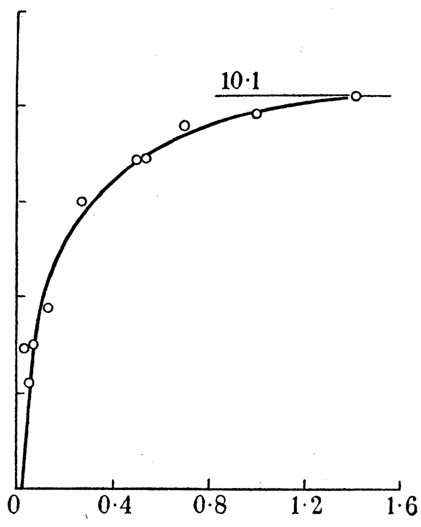


FIGURE 12. *C. chloropyga.* FIGURE 13. *C. albiceps.*

FIGURES 11 TO 13. Relationship between amount of food per larva and puparial size.

The quantitative relationship between puparial length and the weight of meat available for each larva differs as between *Lucilia* and *C. albiceps*. The former has pupae which are longer in relation to breadth than are those of the latter. The differences noted are shown in the following means of measurements of random samples of 200 puparia taken from stock rearings of each of the three species:

species	length (mm.)	breadth (mm.)	ratio length/breadth
L. sericata	8·225	3·806	2·17
C. chloropyga	9.319	4·165	2·24
C. albiceps	8·659	4·182	2·08

It is evident that *C. albiceps* requires the greatest amount of food—more than four times as much as either of the other two species—in order to maintain its maximum puparial size. It does so, in fact, only under conditions where each larva has access to approximately 1·4 g. of meat. The greatest response to an increase in the food supply takes place when the latter is below the level at which 0·2 g. of meat is allowed per larva. Above this point, increasing the food supply results in a comparatively slow response in the form of length increment.

Lucilia and *C. chloropyga* both react to improved conditions much more quickly throughout the range, the former showing an increase in length which occurs more rapidly than in the latter. Both species require approximately the same amount of food per larva in order to produce puparia of maximum size, although the actual sizes differ considerably. This optimum food level is found where concentrations of up to 500 larvae per 140 g. of meat occur.

Thus, if individuals of the largest possible size are taken to indicate optimum conditions of development, it can be concluded that a given population of either *Lucilia* or *C. chloropyga* is able to make much better use of a carcass of a given size than is a comparable population of *C. albiceps*. On this basis alone, *C. albiceps* would require a carcass containing five times the amount of food to produce equivalent results.

Under adverse conditions, *Lucilia* is able to produce relatively larger puparia (and hence larger adults) than can *C. chloropyga*. When only 0·1 g. of meat per larva is available, *Lucilia* can give rise to puparia which are 91 % of the size of the maximum possible; whereas, under the same conditions, the size of the *C. chloropyga* puparium is only 75 % of its possible maximum. At this point, the figure for *C. albiceps* is 77 %, so that here the two Chrysomyias are comparable. After this, however, *C. albiceps* increases much more slowly. At 0·4 g. of meat per larva, for example, it has attained only 91 % of its maximum size, a figure which *Lucilia* finds possible with one-quarter the amount of food.

As far as the relationship between size of puparium and the food available can be taken as a measure, *Lucilia* should be much more successful in its adaptation to intraspecific competition for food than the two remaining species. This superiority will be effective only if there is a definite relationship between size of fly and fecundity.

3. *Effect on fecundity*

The fecundity of a fly is dependent upon its size (Mackerras 1933), so that competition in the larval stage actually governs the potential population of larvae to which any given fly population can give rise.

More exact data for comparative purposes were gained by determining the number of eggs the flies in different size groups could produce at any one time. Oviposition under experimental conditions was so variable that an impossible number of replications would have been needed in order to give satisfactory data. Success in such tests was obtained only in two series in which flies of *C. albiceps* were used. In both, all of the flies laid on the same day and the oviposition data from these can be used as a check on the figures obtained by the method adopted here.

Pupae were sorted into five size groups and were kept singly in glass vials until the flies emerged. An equal number of males and females were put into a cage, each containing one size group. The flies were all kept under similar conditions as regards light, temperature, etc., and were given water, food and two meat meals during the pre-oviposition period. They were not allowed to deposit eggs, the females being removed, killed and dissected at the end of this period. The number of mature eggs found in the ovaries was counted, this being the number that would have been deposited by the fly at the first oviposition. In the extreme size groups (i.e. 6·5 to 7·0 and 9·5 to 10·0 mm.) it was possible to examine only ten females, since the percentage of puparia from a normal population which falls into these groups is very small. In the remainder, very satisfactory samples could be obtained, and these all passed the appropriate statistical tests. The means of all the replications were significant at the 1% point.

The relationship in each of the species is shown in figure 14. There is a well-defined and significant correlation between the size of the fly and the number of eggs which are produced in the ovaries. The assumption that the eggs found on dissection (i.e. the mature eggs in the ovaries) are those which are deposited at the first oviposition is confirmed by the following tests made with *C. albiceps*.

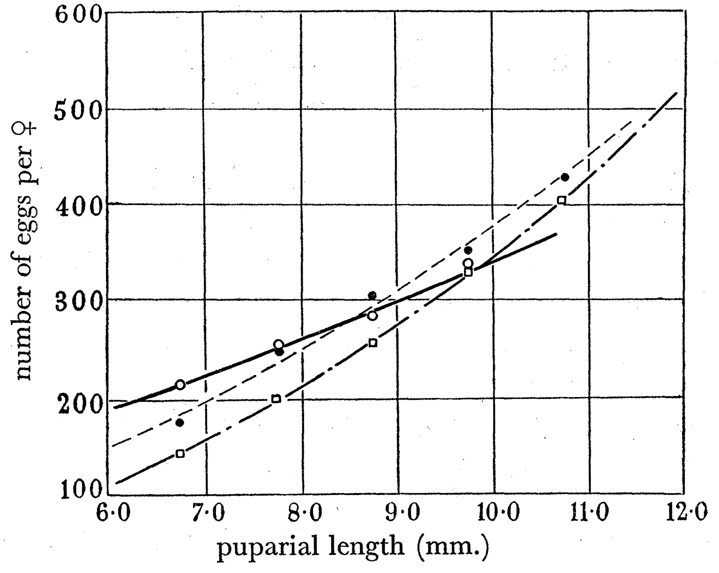


FIGURE 14. Relationship between size of fly and number of eggs in the ovaries. ○, *L. sericata*; ●, *C. chloropyga*; □, *C. albiceps*.

Two series of flies which had emerged from puparia having an average length of 7·25 and 8·75 mm. respectively, were placed in cages, there being six cages of each size, each containing ten females and ten males. All of the females in these series oviposited on the same day, and an average figure for the number of eggs laid at the first oviposition was obtained. In the smaller group (7·25 mm.) there was an average of 180·5 eggs per female. Females of the larger group (8.75 mm.) laid an average of 255 eggs. These two results agree very closely with the figures obtained by dissection.

The goodness of fit of the curves is such that, given the mean puparial length of the population in any series, the mean number of eggs which will be produced by the females in the subsequent population of flies can be ascertained with reasonable accuracy. This has been done for the three species for the various degrees of intraspecific competition (figure 15), the number of eggs per female in each series being plotted against the initial number of larvae on the standard meat ration.

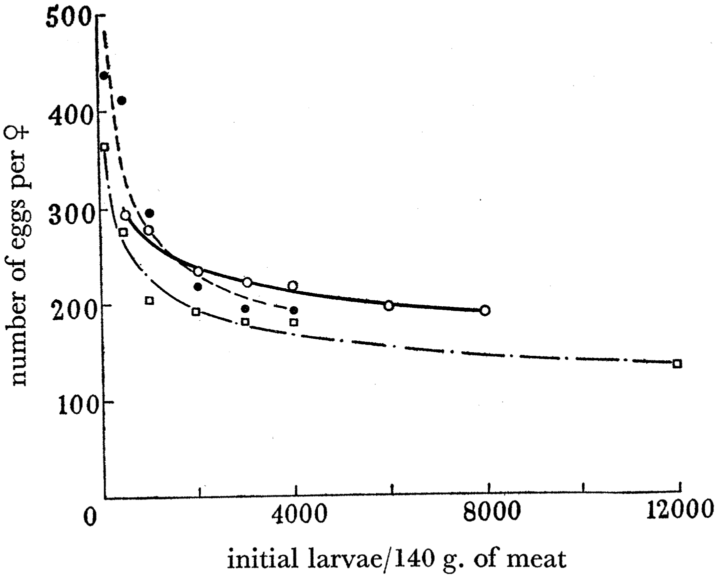


FIGURE 15. Relationship between number of eggs laid per female and initial larval density. Symbols as in figure 14.

The charts (figures 14 and 15) show that the two species of *Chrysomyia* are affected in much the same degree, if the initial difference in the size of the species is taken into account. In the groups giving the larger flies, *C. albiceps* tends to produce slightly more eggs in relation to the size of the female than does *C. chloropyga*, although the latter produces a greater number of eggs throughout. *Lucilia* is clearly not as profoundly affected by change in size. The slope of the *Lucilia* curve more nearly approximates to a straight line (figure 14). The smallest fly is able to lay many more eggs than is the smallest fly of either *C. albiceps* or *C. chloropyga*. On the other hand, medium and large flies of *Lucilia* are much less prolific than are flies in the relative *Chrysomyia* classes.

It is clear that, although *Lucilia* is not as capable of producing large populations under optimum conditions as are the *Chrysomyia* species, it is nevertheless more adapted to adverse conditions engendered by severe larval competition. It has consequently a better chance of survival.

4. *Effect on the sex ratio*

The flies emerging from the puparia in each of the competition series were analyzed for sex.

The degree of competition between the larvae, and hence the amount of food obtained by each larva, had no influence on the sex ratio in any of the three species. This agrees with the findings of the more recent workers.

5. *Effect on total mortality*

The total mortality in a population of flies is divisible into mortality occurring in the egg, larval and pupal stages. A certain degree of mortality in the adult stage cannot be accurately assessed in the field. This will fluctuate according to circumstances and has nothing to do with intraspecific competition for food. It will not be considered here. Mortality during the incubation period will also be ignored. It is usually very low if the eggs do not become desiccated. An adequate moisture content of the meat ensures successful hatching of nearly all fertile eggs. Total mortality will cover the larval and pupal periods and is determined by the number of flies which finally emerge.

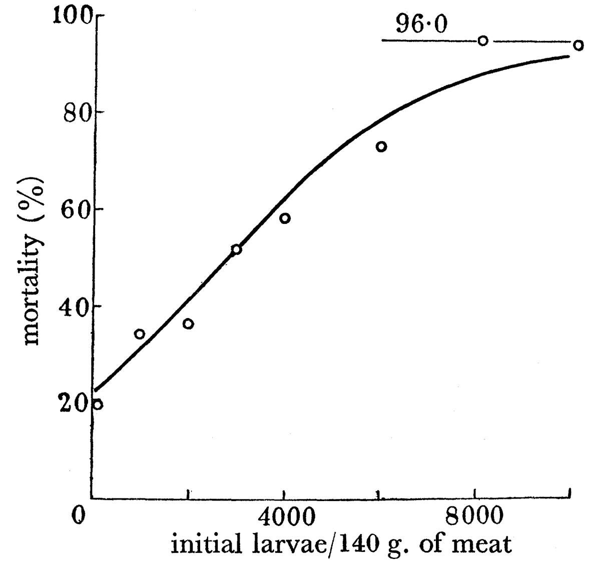


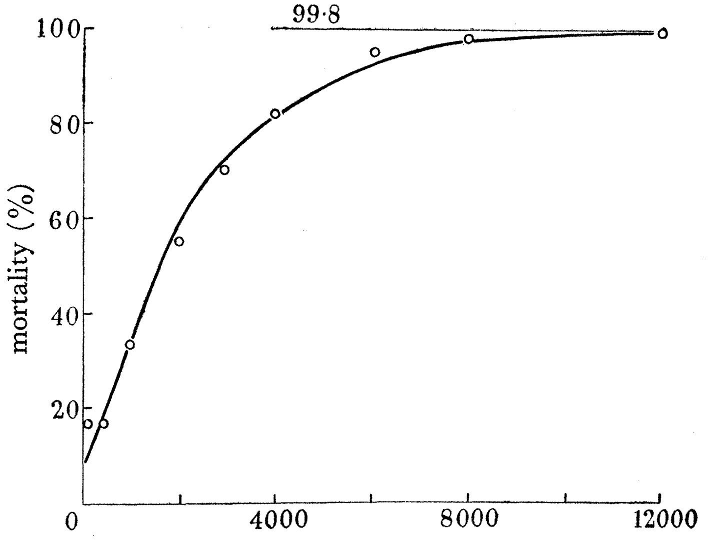
FIGURE 16. *L. sericata*: total mortality as influenced by increasing larval density. $y = \dfrac{96{\cdot}0}{1+e^{1{\cdot}2434-0{\cdot}0004797x}}$.

In all species there is a steady increase in the total mortality with increasing initial larval density in the cultures. The correlation is highly significant in all cases ($P < 0{\cdot}01$). In the case of *Lucilia*, the regression of total mortality on larval density is almost linear, but the observed values are more satisfactorily fitted with a logistic curve (figure 16). The χ^2 test shows that a satisfactory fit is obtained. The regression has a coefficient of $+0{\cdot}9305$ which is significant at $P < 0{\cdot}01$.

The total mortality in populations of *C. albiceps* is represented by a curve in figure 17, the expected values from which give a satisfactory agreement with the observations. The asymptote of the curve is at 99·8 %. Experimental series were carried to a concentration of 20,000 larvae per 140 g. of meat. At this point a mortality of 99·88 % was recorded.

C. albiceps is peculiar among the species studied in that its larvae are cannibalistic. When competition for food is severe, certain individuals in the population are able to survive by feeding upon their less robust companions. In this way, a complete mortality of the population through starvation can never eventuate under the conditions of the experiment. Furthermore, the surviving individuals will all have approximately the same size, since, under severe competition, they will have reached the minimum size which can produce viable pupae.

In the case of *C. chloropyga*, the relation between larval density and total mortality is shown by a curve (figure 18), the theoretical asymptote of which is reached when there is an initial concentration of 10,000 larvae on the standard piece of meat. The observed values show that death of the entire population occurs when there is an initial population of 8000 larvae. With 6000 larvae, a very few survive in some of the replications, but the number is so low that, for all practical purposes, the mortality at this point may be taken as roughly 100 %.



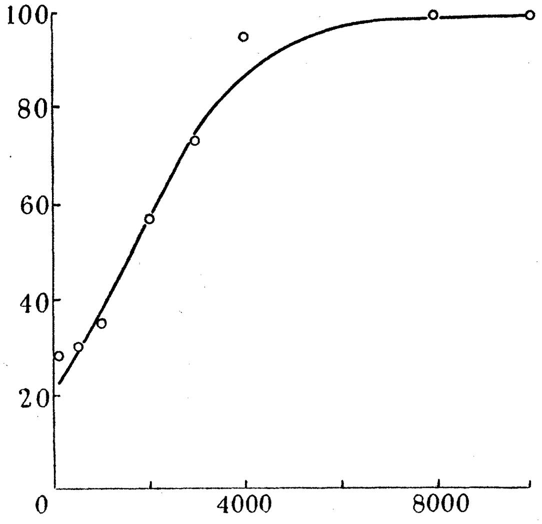


FIGURE 17. FIGURE 18.

FIGURE 17. *C. albiceps*: total mortality as influenced by increasing larval density.

$$y = 99\cdot8(1-\mathrm{e}^{-0\cdot0004251x}).$$

FIGURE 18. *C. chloropyga*: total mortality as influenced by increasing larval density.

$$y = \frac{100}{1+\mathrm{e}^{1\cdot335508-0\cdot0008059x}}.$$

The majority of deaths in the developing population takes place during the larval period. Larvae which have become weakened by malnutrition may form a puparium and even pupate but may die before transformation into the adult fly takes place. A certain degree of mortality during the apparent pupal stage is therefore directly attributable to the result of larval competition. This finding is diametrically opposed to that of Fuller (1934), who claimed that no relationship exists between pupal mortality and competition for food in the larval stage. The data for pupal mortality in populations of *Lucilia* and *C. albiceps* show that there is a definite correlation between these two factors.

When plotted against the initial larval density, the relative percentage pupal mortality in *Lucilia* populations gave points which could be fitted fairly satisfactorily by a curve (figure 19). The regression of mortality on larval density is highly significant, the regression coefficient being $+0\cdot3069$ with a S.E. of 0·05908 and significance at the 1 % level.

In the case of *C. albiceps*, there is a linear regression of pupal mortality on larval density (figure 19) the regression coefficient of $+0\cdot6403$ having a S.E. of 0·0332 and showing significance with $P<0\cdot01$.

The proportion of the pupal population which dies because of insufficient nourishment forms a continuation of deaths during the larval stage arising from this cause. It is thus not necessary to treat pupal mortality as a separate phase, and the effect of competition on the survival of the general population can be computed from the data for total mortality.

The mortality in the combined larval and pupal populations is not all due to competition. When maggots are reared under optimum conditions, where no overcrowding of the medium and hence no competition can possibly occur, a certain percentage of the population dies. In *Lucilia* populations, this mortality was approximately 20 %, approximately 17 % in the case of *C. albiceps*, and 28 % in the case of *C. chloropyga*.

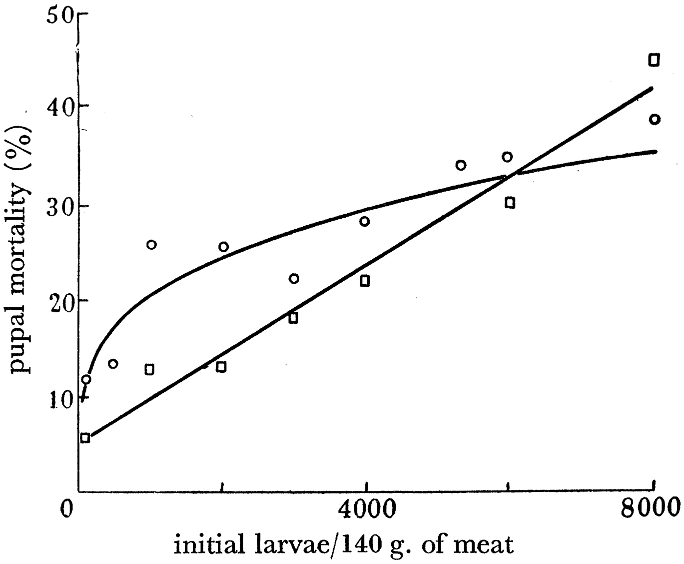


FIGURE 19. Relationship between pupal mortality and initial larval density. ○, *L. sericata*; □, *C. albiceps*.

The cause of this is not known. While it may be due to experimental error, it is most probably a natural mortality which will always be found in populations of these larvae, even under optimum conditions. Since this mortality is independent of the larval density, it should strictly be deducted from the total mortality in each series in order to obtain figures for mortality due to competition. For comparative purposes and for practical computations, however, such an adjustment is not essential.

In all three species, then, total mortality in the populations on a given quantity of food medium is positively correlated with the size of those populations. Moreover, the relationship thus exhibited can be illustrated satisfactorily by means of orthodox curves.

Because of its smaller larvae, *Lucilia* reacts more slowly to an increase in larval density, and the curve for mortality rises less steeply than in the case of *Chrysomyia* species. The curve for *C. chloropyga* more nearly approximates to that for *C. albiceps*, except that it rises slightly more steeply and terminates at 100 % mortality. Because of its predatory habits, *C. albiceps* is never completely destroyed, and its curve ascends very gradually as the asymptote is approached. At the higher larval densities, the total mortality, although high, remains almost constant.

It is clear that *Lucilia* can produce much larger populations of flies from the more dense larval populations than can either *C. albiceps* or *C. chloropyga*. The reasons for this have been advanced under normal larval growth.

6. *The development of larval populations*

It is now possible to go into more detail regarding the manner in which larval populations develop on a piece of meat or on a carcass. In order to make the conclusions more readily applicable to carcasses of any size, the data will be reduced to terms of populations or individuals per gram of meat.

The maximum weight attained by a fully developed larva of each species is obtained from the normal growth weights. Assuming that the standard meat ration was all consumable by the larvae and that the latter require at least the equivalent of their own weight at maturity in the form of food, the following numbers of maximum-sized individuals can be expected to develop on 140 g. of meat: 2349 *Lucilia*, 1759 *C. chloropyga* and 1389 *C. albiceps* larvae. These are equivalent to 16·8, 12·6 and 9·9 larvae per gram of meat respectively. Hence, for optimum development, the numbers of larvae to be used on the meat initially will presumably be those shown here, provided that the preliminary assumptions are correct and that no mortality occurs through extraneous factors.

In the experimental series this expectation was not realized. Numbers of larvae very nearly equal to the expected numbers were obtained, but the larvae in these populations were not of the mean maximum size for the species as was assumed, nor were they obtained by using initial concentrations of larvae anywhere approaching those postulated.

The actual numbers obtained which most nearly agreed with the expected numbers were: 2326 *Lucilia*, 1572 *C. chloropyga* and 1188 *C. albiceps*. These represent 16·6, 11·2 and 9·2 larvae per gram of meat respectively, figures superficially very close to the theoretical ones. But these larvae were produced from initial populations of 28·5, 14·3 and 14·3 larvae per gram of meat, numbers considerably in excess of the postulated ones. Since the larvae which actually survived to form pupae were significantly smaller than the mean maximum size, a loss in population mass (not numbers) occurs which is reflected in both the mortality and size. The relevant figures are compared in table 2.

TABLE 2. COMPARISON BETWEEN EXPECTED AND OBSERVED LARVAL POPULATIONS PER GRAM ON 140 g. OF MEAT

	expected population per g.			observed population per g.			
species	initial	final	pupal length (mm.)	initial	final	pupal length (mm.)	mortality (%)
L. sericata	16·8	16·8	8·76	28·5	16·6	6·86	42
C. chloropyga	12·6	12·6	10·39	14·3	11·2	7·48	21
C. albiceps	9·9	9·9	10·17	14·3	9·2	7·17	40

It is evident that the following losses occurred in the experimental series:

(1) A reduction in size of the individuals and hence a loss in the total weight of the population as determined by the weight of the individuals which survive to pupate.

(2) A loss in numbers through mortality.

It is thus possible to find populations which attain to the theoretical maximum number of individuals, but only where this is achieved at the expense of the size of the individuals and by increased mortality. A number of factors contribute to produce this phenomenon, which is peculiar from the fact that the expected final population density is realized when many more than the optimum number of individuals are originally present on the meat. This indicates that the larvae of the flies in question are unable to make the best use of the food available. The following are the main factors concerned.

Factors causing loss

(i) *Unconsumable food.* The gross ration of meat supplied does not represent the amount of food available for larval nutrition. A certain proportion is unconsumable, and the standard ration cannot support as many individuals to full development as was assumed above. Blowfly maggots feed mainly on the proteins of the meat, the fat and sinew not being used. Short of a complete chemical analysis of all the meat used, together with a physiological test of the exact diet of the larvae, procedures not possible during the present investigations, a measure of the unconsumable portion of the meat can be obtained indirectly from the data available.

In the *Lucilia* series in which there was an initial larval population of 2000 per 140 g. of meat the number of pupae formed was 1732. This represents larvae able to complete their development. During the larval period there was an experimental or basic mortality of 9 %, with a further mortality, due to competition, of 4·4 %. The mean pupal length in the series was 7·26 mm., which, by interpolation (figure 7), is found to be equivalent to a weight of 0·0385 g. per pupa. The mean maximum pupal length for all the *Lucilia* series was 8·76 mm., which is equivalent to a weight of 0·0510 g. per pupa. There is thus a loss in the series of 24·5 % in pupal weight. It follows that the number of larvae which survived in the series was equal to 1732 minus 24·5 % of this number, or 1308 larvae of maximum weight.

If all of the meat supplied to cultures is consumable, then it could produce 2349 larvae of full size and weight (*vide supra*). Since there is always a basic mortality of 9 %, this number will be reduced to 2138.

But all of the meat is clearly not acceptable as food, and the unconsumable portion will be reflected in the difference between the number of larvae expected were it all consumable and that actually obtained. Thus, 2138 minus 1308 gives 830 larvae which represents a decrease of 38·8 %. This figure may be taken as a measure of the unconsumable portion of the meat. Hence, in this case, only 86 out of the 140 g. of meat supplied were available as food.

The percentage available will vary with the quality of the meat used. In the *Lucilia* series, calculations were made for all larval densities used. These gave values ranging from 29 to 44 % with a mean of approximately 37 %. Generally speaking, therefore, only 88 g. of consumable meat were contained in the gross ration normally supplied in the experiments.

The fluctuating quality of the meat obtainable introduces an unavoidable source of experimental error throughout. On the whole, the error is not a serious one, since it is largely cancelled out by the replication method. It probably contributed to occasional discrepancies which appeared.

(ii) *Excess of requirements over larval weight.* The assumption that the weight of a fully grown larva indicates its total requirements in food material provided a basis upon which to work. This is not entirely correct, and the weight of food needed for the complete development of a blowfly maggot is more likely to exceed its weight when mature. A certain proportion of the food ingested by an animal is excreted unchanged; some is partially absorbed, the remainder being excreted in liquid form, and so on. The total amount of material used by the larva is not necessarily added to its continually increasing body weight. The excess of weight of material over body weight will therefore partially account for the discrepancy noted in the previous section.

(iii) *Reduction in size.* The general tendency in populations of larvae is to produce as many *individuals* which will survive to form viable pupae as the meat available will allow, even though it means a drastic reduction in the *size* of the individuals to a minimum. Faced with a shortage of food, the population as a whole sacrifices size of individuals in favour of numbers. With increasing larval density on a given quantity of medium, it is only when the minimum pupal size for the species is reached that the numbers of larvae which pupate begin to decrease instead of increase. This is clearly illustrated by the figures for the development of *Lucilia* populations when there are 88 g. of consumable meat (figure 20).

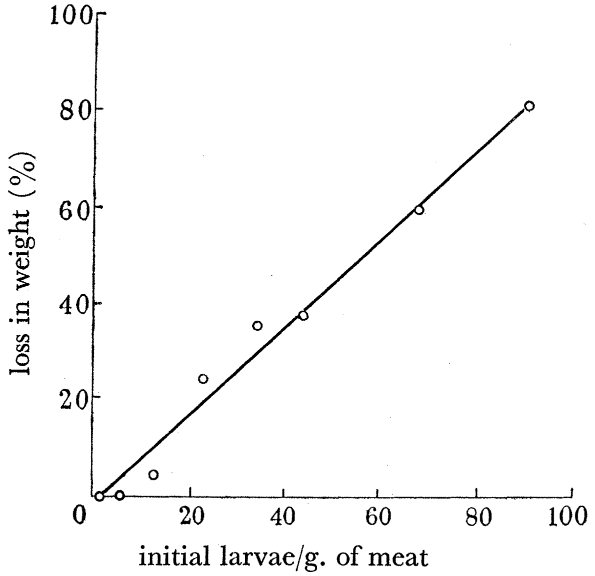


FIGURE 20. *L. sericata*: percentage loss in pupal weight as a result of competition for food.

As a measure of population growth, size of individuals gives a picture very different from either total mass or actual numbers. While the size of the individuals in a population decreases, the number of individuals increases and the total mass tends to remain approximately constant up to a point. Reduction in size thus forms an adaptation to adverse conditions which allows more individuals to develop on a given quantity of food than would otherwise be possible. Although the resultant flies may be a population of C3 individuals and the females will lay fewer eggs than do those of maximum size, it is still capable of producing a sufficient number of progeny to give rise to a relatively large and, given suitable conditions, healthy succeeding generation. Furthermore, this adaptation ensures the production of an adult population sufficiently large to effect dispersal over a wide area.

The linear regression illustrated in figure 20 shows this clearly. The loss in weight shows a definite correlation with the increase in the initial population per gram of meat. There is a limit to the reduction in size, since larvae which do not attain a certain growth weight are unable to pupate. This minimum size varies with the different species and can be ascertained from the frequency distributions. When the larval population as a whole reaches this point, any further increase in the degree of competition for food can only increase the mortality in the population. The number of individuals able to pupate then decreases while the total mass (biomass) of the population also decreases. During this process, the survival curve falls very sharply for all three species.

(iv) *Mortality.* Theoretically it should be possible for a population of 16·8 maximum-sized *Lucilia* larvae to develop on 1 g. of consumable meat. This number is attained in one series only where an initial population of 45·6 larvae/g. was present. The final population was 26·43 larvae/g., but these were 36·7 % below the full size. There was thus a high mortality combined with a considerable reduction in size.

As noted previously, there is a positive correlation between mortality and the density of the population, the numbers of deaths increasing in geometrical progression as the number of larvae per gram of meat is increased. This behaviour of mortality accounts, in a large measure, for the fact that, in order to obtain a maximum production of larvae by weight, there must be an inordinately high initial larval population. In the case just quoted, although the expected production from 1 g. of meat is 16·8 larvae, it requires nearly three times this number in the original population to achieve this result.

Larvae tend to congregate in more or less large, densely packed groups under the meat. A certain proportion of the individuals tends to be crowded out and pushed away from the food, particularly where there is a high larval density. Such individuals probably succumb later, even though sufficient food remains to enable them to complete their development. Except at very high initial densities, where practically the whole of the underside of the meat is occupied, there is always an appreciable residue of food after the majority of the larvae have pupated. In addition, very small larvae, which have never developed far, are to be observed. These larvae never survive to pupate.

The congregation of the larvae in masses ensures a plentiful supply of secretions for the predigestion of the meat. Where larvae are crowded out or where they become isolated or are in small groups, mortality increases. It seems that single larvae are unable to produce enough digestive fluid to obtain sufficient food by themselves.

(v) *Combined loss.* Mortality and decrease in size and weight of individuals in a population of maggots are closely correlated as direct results of larval competition for food. There is a highly significant correlation in which $r = +0{\cdot}9794$ and $P < 0{\cdot}01$. The regression of loss of weight on mortality, which is a linear one, is shown in figure 21. The full effect of competition on the larval population is obviously not represented by isolated data. Mortality alone, or loss of weight alone, are only partial effects. To obtain the complete account of loss through overcrowding of individuals on the medium, it is necessary to include both of these together with the final effect on the potential production of viable eggs in the subsequent population of adult flies.

In the series of *Lucilia* in which the initial larval density was 2000 on the standard meat ration, the total mortality was 36 % and the loss in pupal weight over the maximum was 24·5 %. The actual number of deaths was 720, leaving 1280 survivors which pupated. The weight of a pupa of mean maximum size is 0·0510 g., so that 2000 individuals of this size would weigh 102 g. The weight of the 720 casualties would have been 36·72 g. The percentage loss of weight by death in the population is therefore 36, a figure which agrees with the percentage mortality as determined by the number of larvae which died. Each of the

1280 survivors weighed only 0·0385 g., since they were below the mean maximum size. The total weight of survivors is therefore 49·28 g. The loss in weight to the population through death and decrease in size combined is therefore 102 − 49·28 = 52·7 g. approximately. This is equivalent to 51·6 % total loss in population mass.

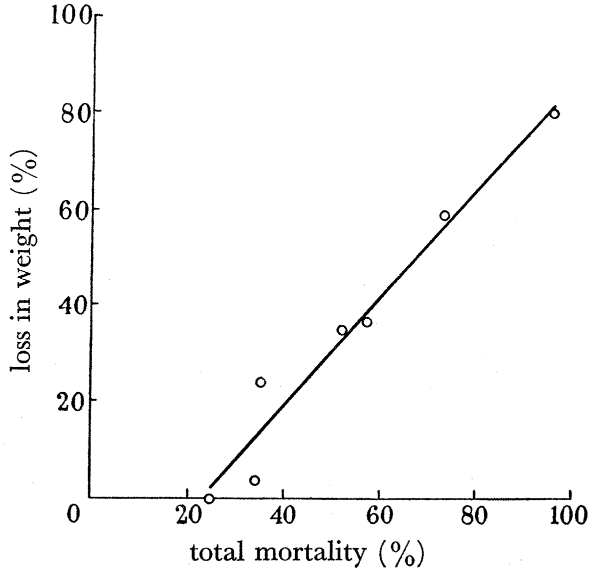


FIGURE 21. *L. sericata*: regression of percentage loss in pupal weight on percentage total mortality in pure cultures.

If all the larvae had survived and had produced adults, there would have been approximately 1000 females which, if of full size, would have laid 292 eggs each at their first oviposition. The total number of eggs at this first laying by the population of flies would thus have been about 292,000. But there were only 1280 flies, approximately half of which were females. These were not of the maximum size and were capable of laying only 232 eggs each, giving a total from the whole population of 148,480 eggs—a loss in potential production of approximately 143,520 eggs as a direct result of competition. This is equivalent to a 48·9 % loss in potential progeny which is an appreciable loss to the general population of the species in any given area.

The loss as expressed by percentage of potential progeny is not quite as great as that in total mass of population. Expressed as a difference in percentages this is not impressive, being only 2·7, but, in terms of the number of eggs involved, it is appreciable, being equivalent to 8760 eggs. In other series, an even greater difference in potentials will be found. The adaptation to adverse conditions, whereby the oviposition of the flies is not as severely affected by larval competition as is the average size of individuals and the percentage survival of the population, should be noted.

The loss in potential egg production gives the best measure of the effect of competition since it includes both mortality and size reduction. It is the potential number of progeny that can be produced by a population of flies which is ultimately important, both for the species in the struggle for existence and for practical control. Where a species is highly adapted to withstand adverse conditions, the problem of control becomes proportionately more difficult as its population decreases. A fly such as *Lucilia*, which is comparatively little affected by size in the production of eggs, will be able to increase its population with great rapidity after suffering the most severe of setbacks.

Thus, it is not necessary to postulate a large population of flies in the field in order to account for an outbreak of strike among sheep or a sudden increase of breeding on carrion. Comparatively few flies in a given area can produce either phenomenon whatever the size of the individual flies may be. Although the parent fly is subnormal in size, it is only the number of eggs which it can produce that is affected. They give rise to larvae which are healthy, of normal size and which will, given the opportunity, produce pupae and adults which tend to conform to the mean maximum size for the species. Thus recovery from adverse conditions can be complete and immediate.

The above discussion of loss has been confined to *Lucilia* populations purely for the sake of brevity and continuity. Similar loss occurs in populations of the *Chrysomyia* species and does not require further special discussion here. In the case of *C. albiceps* its cannibalistic tendencies, at times, give rise to an increase in mortality but tend to check the loss due to reduction in size. The habit also acts in some degree as an adaptation to adverse conditions. During shortage of food, certain individuals survive by feeding upon the weaker members of the population. By this means they not only obtain enough nourishment to enable them to survive, but are often able to attain to a larger size than would be possible in non-cannibalistic species. There is thus practically never a crisis in which all individuals may become starved to death as could arise otherwise. This crisis, for example, becomes evident at a comparatively low larval density in the case of *C. chloropyga.*

7. *A comparison between the species*

The relative success of the three species of blowflies under varying degrees of intraspecific competition for food can be judged from a consideration of two distinct but related aspects, viz. (1) the efficiency with which the developing larval population, as a whole, can make use of the available and consumable food supply; and (2) the actual density of the fly population which is ultimately produced, together with its fecundity and hence the potential larval population to which it can give rise.

The adult population density depends upon the amount of food which is available to the preceding larval population and upon how this is utilized. In this way, the two aspects of the problem are interdependent. On the other hand, a comparison between two populations involving the total weight of larvae (i.e. the biomass) to which a given quantity of medium can give rise will not necessarily offer any indication of the potential fly population which will follow, nor of the relative abilities of the two species to maintain their general populations at a high level in the field. In this respect, comparisons of the biomass produced by each species from a standard food supply are less useful than comparisons of the total fly populations and their potential progeny.

(1) *Utilization of the medium.* The efficiency with which the food is used will be shown by the total mass of the population which can be produced on a given quantity. Since the three species of blowflies vary somewhat widely in their total food requirements per larva and in their maximum weights when mature, a bare statement of the biomass would give no information as to the relative success of any one species. Although the mass may be the same for any two populations, the number of individuals comprising them may be very

different. A more satisfactory comparison is obtained by reducing the data for the different species to a common denominator.

The figures for larval survival have been expressed, in all three cases, in terms of an equivalent number of maximum-sized *Lucilia* larvae per gram of consumable meat. This is readily calculated from the ratio of growth weights of the larvae and from the known relationship between puparial length and weight. The result is seen in figure 22, where the different degrees of initial larval density are also given in *Lucilia* equivalents. Up to an initial concentration of approximately 40 *Lucilia* equivalents/g. of meat, there is little difference between the species in the efficiency with which they utilize the food. All produce approximately the same mass of population, with *C. albiceps* being slightly inferior to the other two species. From this point, an increase in initial density results in a reversal of positions between the two *Chrysomyia* species, *C. chloropyga* suffering a rapid deterioration in its ability to maintain its population level. *Lucilia* remains superior to both. The decline of *C. chloropyga* continues until complete mortality supervenes, when approximately 90 *Lucilia* equivalents are initially present on the meat. The positions of the curves for *Lucilia* and *C. albiceps* become reversed at an initial concentration of 70 *Lucilia* equivalents, so that the latter species now assumes the superiority formerly evinced by *Lucilia*.

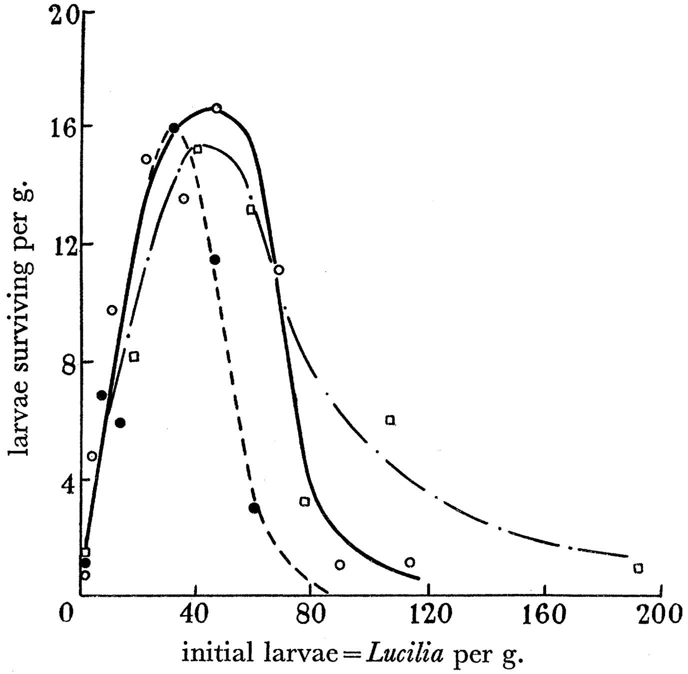


FIGURE 22. Survival of larvae per gram of consumable meat. Larvae of all species expressed as the equivalent of maximum-sized *Lucilia* larvae. ○, *L. sericata*; ●, *C. chloropyga*; □, *C. albiceps*.

The ability to maintain the population through efficient use of the medium under adverse conditions clearly varies widely among the species. The failure of *C. chloropyga* occurs comparatively early and is probably due, in part, to the fact that its larvae are much more sensitive to the mechanical effects of overcrowding than are those of *Lucilia* and *C. albiceps*. As a result, many more of the immature larvae crawl away, or are forced away from the food and, after wandering about on the outskirts of the seething population of their fellows, subsequently die from starvation. This was noted continually in cultures where the higher initial concentrations of larvae were used. There was no obvious connexion between this and the condition of the medium at the time, nor did external conditions appear to affect the issue to any great extent.

Larvae of *C. chloropyga* increase in growth weight at approximately the same rate as *Lucilia* larvae, whereas *C. albiceps* larvae increase much more rapidly (*vide supra*). Moreover, *C. chloropyga* larvae take a much longer period in which to attain their maximum weight than do those of either of the other two species. They are therefore exposed to adverse conditions for a longer period and are thus at a disadvantage in comparison with *Lucilia* and *C. albiceps*.

The relatively higher survival of *C. albiceps* larvae at the higher initial concentrations is explained by cannibalism. By this means, there are always a few survivors even with the most severe overcrowding. A certain degree of cannibalism is present in all populations, although it is not as rife in those provided with ample food per larva. It is no doubt responsible for the slightly lower survival of the species at the lower initial densities as compared with *Lucilia* and *C. chloropyga*.

If this cannibalism is allowed for in assessing the results of intraspecific competition, it would seem that *Lucilia* and *C. albiceps* larvae are approximately equal in respect to efficiency in dealing with the available medium. *C. chloropyga* is comparatively inefficient and is thereby less able to withstand the adverse conditions of overcrowding.

(2) *Population potentials.* The criterion of the success of a species must be its ability to produce a large number of offspring in the succeeding generation. This will depend upon the total number of flies from the given quantity of medium and upon the size of the individuals so produced. The potential number of eggs from a population reared upon 1 g. of meat will give the most reliable indication of the success of the species in the competition for food. When this is calculated for the three species and the results are plotted against the initial larval densities, the curves in figure 23 are obtained.

Given a limited quantity of consumable food and intraspecific competition, *Lucilia* produces a potential future generation per gram of medium far in excess of that which is produced under similar conditions by either of the *Chrysomyia* species. The three species are approximately equivalent at the lower initial larval densities, but when these are increased, the potential egg production of *Lucilia* at once exceeds the other two. The maximum of its curve occurs at a higher initial density than that of the Chrysomyias.

C. chloropyga produces slightly more eggs than *C. albiceps*, except at the higher initial concentrations. At 4000 larvae per 140 g. of meat, the two *Chrysomyia* species are approximately equal; after this point, *C. chloropyga* falls off, mainly owing to increased mortality. Production of *C. albiceps* is maintained by means of cannibalism.

The picture obtained from egg-production figures is very different from that given when using the biomass as a means of comparison. In terms of the ability to maintain a large population in the field, *Lucilia* is by far the most successful species under conditions of intraspecific competition. It is much better adapted to withstand the adverse effects which are engendered, especially with respect to the relationship between size and fecundity. More flies are produced when the larval population is overcrowded, and these, though small, can produce a comparatively greater number of eggs per female than those of *C. albiceps* and *C. chloropyga* of comparable size.

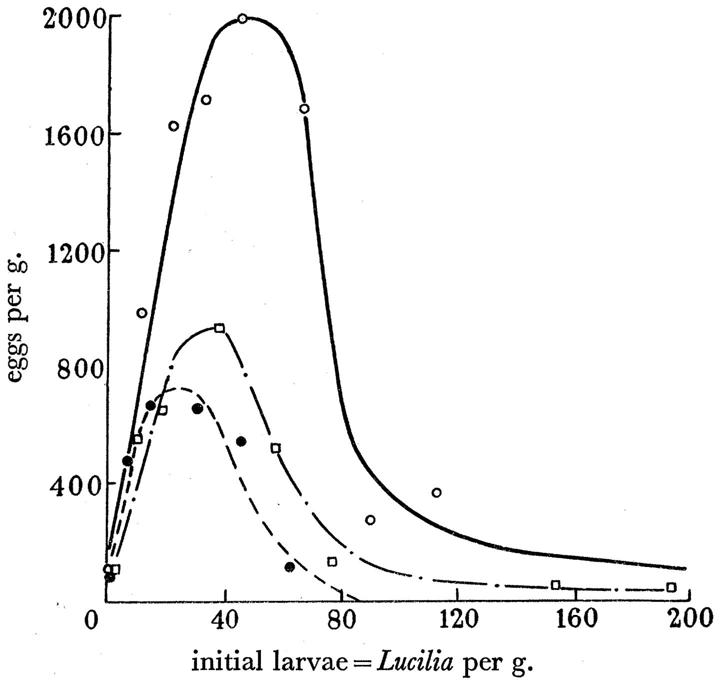


FIGURE 23. Potential number of eggs produced per gram of consumable meat in intraspecific competition. Symbols as in figure 22.

8. *Competition and population fluctuations*

If intraspecific competition for food were the sole limiting factor in populations of flies, and if the quantity and quality of the food remained constant from generation to generation, violent fluctuations in the populations of adult flies present in the field would occur. Because of this, it could never constitute a reliable control factor, since it could not prevent the flies concerned from assuming epidemic proportions periodically. This is easily demonstrated by simple calculations from the data given.

If, in any one generation of larvae, intense competition prevails, there will be a high mortality, a reduction in the size of the resulting flies and a reduced egg production. A smaller larval population will follow in the ensuing generation, and this, given the same quantity of consumable medium, will suffer less intense competition, so that either more or larger flies will be produced. These will give a greatly increased number of eggs. The larvae from these will again suffer intense competition. A series of cycles will thus be set up in which periods of scarcity will succeed periods in which the flies are extremely numerous and in which they will cause extensive damage.

In a fly such as *Lucilia*, where adaptations for withstanding adverse conditions exist, the full effect of competition will probably not occur during the course of a single generation. There will be a lag of one or more generations between the peaks of abundance. Fluctuations in population density will also be influenced by the availability of carrion. In the field the food supply will rarely, if ever, remain constant. The relationship between the adult fly population and the amount of available food present at any one time will largely govern the degree of larval competition and hence the degree of limitation of the population. Since this factor is unpredictable, it is not possible to extend the argument.

9. *Summary of effects of intraspecific competition*

A detailed examination of the effects produced by intraspecific competition has shown that, with increasing degrees of overcrowding, the following effects on the population are observed with each species:

(1) An increased mortality in the larval population which is positively correlated with the increasing density and follows a well-defined course.

(2) An increase in the pupal mortality, similarly correlated with larval density.

(3) A decrease in the size of the maturing larvae and hence in the puparial length.

(4) A decrease in the size of the adult flies which arise from these pupae follows.

(5) A decrease in fecundity of the flies, positively correlated with the decrease in size and found to follow a well-defined course peculiar to the species concerned.

Throughout, there is a tendency to sacrifice size of individuals to increase in numbers and, in all cases, the mean size of the maturing populations tends towards a minimum size with increasing degrees of overcrowding on the larval medium. This attempt to compensate for a shortage of food is not altogether successful, since the total mortality in the population also increases with an increase in density, and this takes place from the very earliest stages in the competition. The two effects—increase in mortality and decrease in size—proceed simultaneously and are complementary sources of loss to the general fly population.

Populations of *L. sericata* suffer less from the ill-effects of intraspecific competition than do populations of the two *Chrysomyia* species. This holds good over the whole range of larval densities used in the experiments. The explanation of this superiority in survival value is to be found in a combination of factors. These are:

(*a*) A smaller maximum larval growth weight, which makes it possible for more larvae to be reared upon a given quantity of medium.

(*b*) A shorter growing period which ensures a greater chance of completing growth before the onset of deterioration in the medium.

(*c*) The capacity of the flies in the smaller size groups for producing a larger number of eggs than do flies in the corresponding size groups of the *Chrysomyia* species.

The first two of these lead to a lower total mortality at any given larval density, so that, when combined with (*c*), the outcome of these adaptations is a higher potential population than is the case with either *C. albiceps* or *C. chloropyga.*

The two Chrysomyias reach a high mortality figure at comparatively low initial concentrations of larvae. Of the two, *C. chloropyga* soon suffers complete elimination through competition under the conditions of the experiments; while *C. albiceps* maintains a small survival value throughout the higher concentrations only by the adoption of cannibalism.

If intraspecific competition for an available food supply were the only limiting factor in populations of larvae, *Lucilia* would be able to maintain a high level of population density and might be expected to be even more prevalent in nature than it is at present. This population density would exhibit a periodic function with alternating periods of scarcity and high abundance. The Chrysomyias would be less abundant, with *C. chloropyga* tending to extermination.

VI. Interspecific competition

The comparatively simple case of intraspecific competition will rarely be encountered in nature. It is more usual to find two or more species inhabiting the same carcass simultaneously or following one another in the ecological succession so closely that their populations overlap in time. When this occurs, interspecific competition for the available food supply intervenes.

Blowfly eggs are usually laid in large numbers on any carrion which is left exposed in the field and the competition among the resulting larval populations is therefore severe. Seasonal variations in the populations of adult flies render it unlikely that all three of the species dealt with here will occur in even approximately equal numbers at any one time, although there will be occasions on which a threefold struggle between their larvae will take place. It is therefore more usual for competition to occur mainly between larvae of two species only.

It is no longer simply a case of a struggle for existence between individuals which, ostensibly at least, commence life with equal chances of survival. Specific peculiarities now make themselves apparent and introduce differences which may be prejudicial either to the species possessing them or to one or another of the competing larval populations as a whole. The relevant population therefore suffers to an extent depending upon the degree of bias which such peculiarities tend to induce.

Since interspecific competition takes place primarily for food which is strictly limited in supply, it is essentially a special form of the intraspecific struggle. This it includes as an integral part of the phenomenon. The gross effects on the population of insects concerned will differ from those of intraspecific competition by reason of specific adaptations. The majority of these have become evident, and the outcome of interspecific competition between any of the three species under review could be predicted in a very general way by assuming their interactions when brought into direct conflict. Experimental data will provide more accurate information, since the effect of two different species inhabiting the same medium will not always or necessarily fulfil these expectations.

1. *Method*

The general technique described earlier was used in the present series of experiments. The standard gross ration of 140 g. of fresh, lean beef was retained. Newly hatched larvae of each of the species used in any one experiment were placed at once on the meat in the numbers required. Those destined for the same piece of meat were dealt with at the same time. There was therefore a slight difference in the ages of the maggots as between species. For the purpose of obtaining eggs, fresh meat was exposed in the fly cages at the same time during the day, and each species laid on its particular piece of meat in its natural sequence. The maggots hatched in the same order. Flies of *Lucilia* usually oviposited approximately 1 hr. before those of *C. chloropyga* and the latter 1 hr. before *C. albiceps*. As the incubation period of the eggs is roughly the same in all cases, the difference in larval ages when experiments were commenced corresponded to the difference between the times of oviposition by the respective flies.

Two factors were eliminated in the experiments. No previous feeding had occurred on the medium and there was therefore no prior 'conditioning' by one or another of the species.

Similarly, no diminution of the food supply had occurred as a result of feeding by an earlier population. By the method adopted, it was possible to ensure results which could be regarded as purely effects of competition between the species as far as it is possible to isolate this phenomenon. Records of the final populations and of mortality and size were kept as before.

2. *Competition for food between two species*

(*a*) *Lucilia sericata* and *Chrysomyia chloropyga*

In the Karroo sheep-breeding areas, these two blowflies show a marked coincidence between their periods of greatest abundance (see Smit 1931, p. 330; Hepburn 1943*b*, p. 71). Their larval populations normally compete for the available carrion upon which the greater proportion of the field populations of the flies is raised. There will be occasions, mainly during the spring months, when they will be the only contestants for the common food supply. At this time the simplest form of interspecific competition exists, since neither species is predatory in habit. As the season advances and the adult fly populations increase and reach their peaks of abundance, competition increases in severity. At the same time, other species arrive on the scene and the situation becomes more complicated.

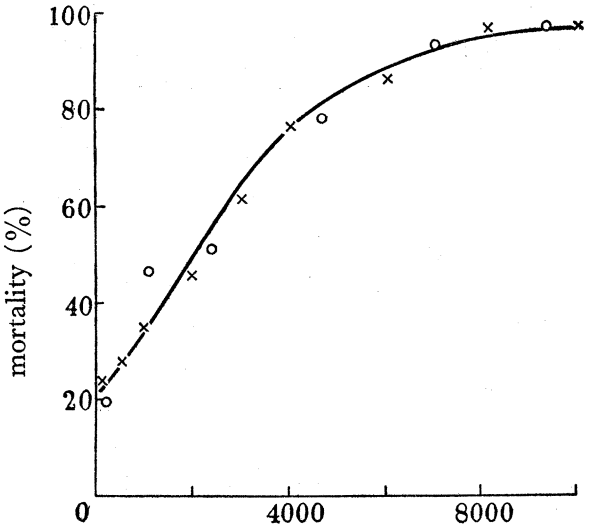
In order to reproduce conditions approximating to those of the earlier period, a series of mixed populations containing equal numbers of each of the two species was set up. The series extended from 100 to 10,000 larvae of each species. These were treated as described for intraspecific competition. In order to compare the present results with those obtained through intraspecific competition, the data must be adjusted for the extra numbers of larvae present as well as for the specific difference in weight which will influence the amount of food consumed per larva. In the following account this has been done by expressing the total population of the larvae in terms of *Lucilia* equivalents.

(i) *Mortality in the mixed population.* If the total mortality for each species is compared with that for the same species under intraspecific competition at comparable initial concentrations of larvae, a marked difference is noted. On the whole, the *Lucilia* mortality in the present series is higher, while the *C. chloropyga* mortality is lower than in the intraspecific series. This is to be expected, since there are now two different species of very different growth weights inhabiting the same piece of meat. If the intraspecific series having an initial population of 2000 larvae is compared with the interspecific series in which 1000 larvae of each species were used, there will be the same total *number* of larvae but not the same *mass*.

The *C. chloropyga* population in the interspecific series was reduced to terms of an equivalent *Lucilia* population in each case, and the mortality in the total mixed population of the two species was calculated on this basis. The figures so obtained can be used in a comparison with either the *Lucilia* intraspecific series or that for *C. chloropyga* when the latter has been similarly transposed.

The intraspecific data for *C. chloropyga* were treated in this way and were combined with the comparable *Lucilia* series, the percentages of mortality being averaged in each case. The figures obtained were plotted against the averages of the expected values. The mortality for the mixed population was plotted on the same chart (figure 24).

The average curve for mortality in pure culture of the two species fits the values for the mortality in mixed populations very closely. When related to the quantity of consumable food which is available, this striking agreement points to the conclusion that the effect of interspecific competition between *Lucilia* and *C. chloropyga* is merely an additive effect of the operation of intraspecific competition in the two populations. As in the latter phenomenon, the outcome is governed by the ratio of quantity of food to the mass of individuals consuming it and apparently by no other factor. There is seemingly no direct effect of one species upon another, such as the crowding out by a more robust or quicker-growing species, as suggested by other workers.



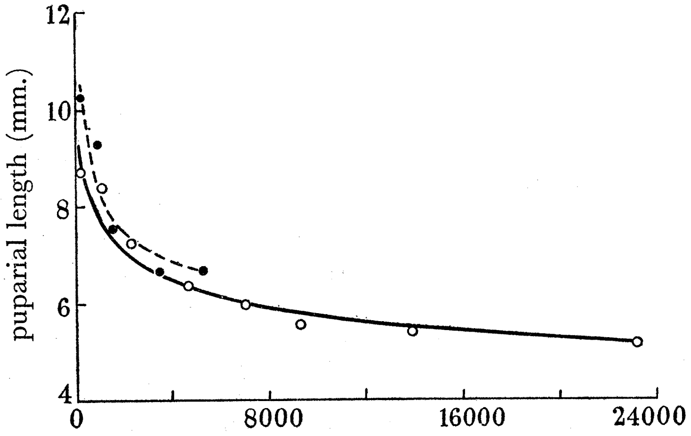


FIGURE 24.

FIGURE 25.

FIGURE 24. Total mortality in mixed populations of *Lucilia* and *C. chloropyga* plotted with the curve for the mean expected values for mortality for the two species when in pure cultures. o, observed mortality in the mixed population; ×, mean of observed values in pure cultures.

FIGURE 25. Puparial size as affected by competition for food in mixed populations of *Lucilia* and *C. chloropyga*. o, *L. sericata*; ●, *C. chloropyga*.

Before discussing this in more detail it is desirable to put forward confirmatory data from two other aspects of competition already noticed in the intraspecific series of experiments. These are the effect of overcrowding on the size of the surviving individuals and on the fecundity of the resulting adults and hence on the potential future generation of the insects concerned.

(ii) *Reduction in size.* This was ascertained from the puparial lengths in the surviving population using the frequency distributions of these measurements. The mean lengths in each series are plotted in figure 25, the *C. chloropyga* data being related to the appropriate *Lucilia* equivalents of the mixed population concerned (for data for intraspecific competition cf. figures 11 and 12). The observed values for the two species are readily fitted with simple curves of the relative growth type. In both cases the tests for goodness of fit gave probabilities exceeding 99 %.

In the *Lucilia* curve, which continues longer than that for *C. chloropyga*, since the latter species suffers elimination when the initial mixed population exceeds 5000, the rapid decline in puparial length observed in the lower density range as the population increases is succeeded by a more gradual decrease as the mean minimum puparial size for the species is approached. The similarity to the intraspecific curves in both species is as striking as was the resemblance in the case of mortality data. In fact, so close is the agreement that, if the data for puparial mean sizes in the intraspecific series are plotted on the same figure with the interspecific values, the observed values for *Lucilia* and *C. chloropyga* in the former will fall extremely close to the respective curves for the two species in mixed populations.

The reduction in size of the individuals in the mixed populations as related to increasing initial larval density clearly follows the same law, whether the species are feeding alone or in company. The effects obtained in the mixed population are derived from the sum of the effects of competition in the two separate populations of which it is composed. The presence of a second species has no influence upon either as regards reduction in size.

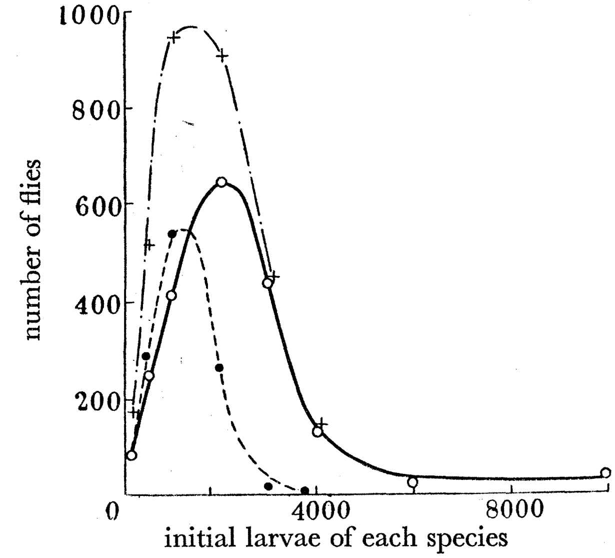


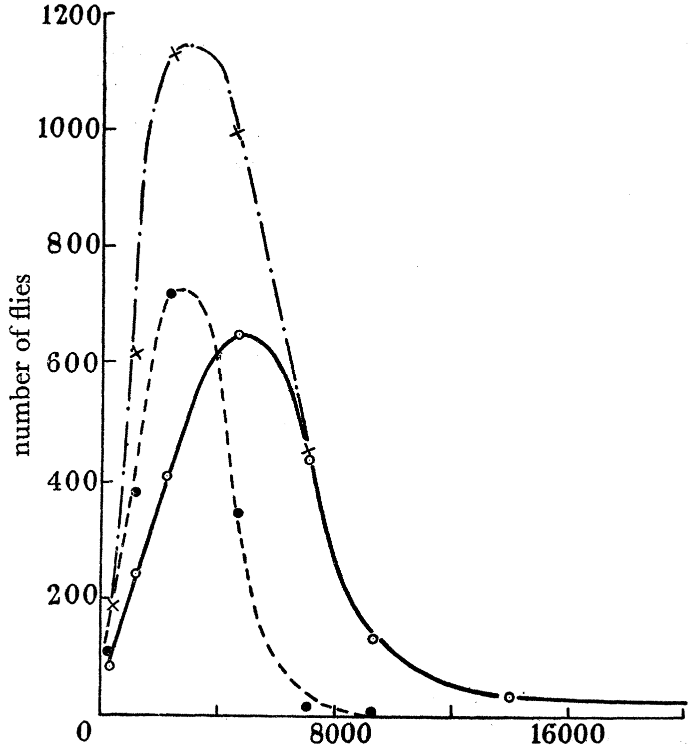
FIGURE 26. Total actual number of flies of each species emerging from mixed larval populations of *Lucilia* and *C. chloropyga*. ○, *L. sericata*; ●, *C. chloropyga*; +, total flies.

(iii) *Reduction in fecundity*. Since the reduction in size of puparia in the mixed population is similar to that obtaining under comparable conditions in pure cultures of the two species, it follows that the capacity for oviposition of the flies arising from the mixed populations will also exhibit a close agreement. Up to now the two species on the common food medium have been treated as one population and the number of individuals expressed in *Lucilia* equivalents. Since adult flies show a specific difference in the relationship between oviposition and size, no simple conversion can be used here. The actual numbers of flies and eggs will therefore be taken.

The population of flies of the two species which emerged in the series is plotted in figures 26 and 27; the potential egg production of these flies, expressed as numbers produced per gram of food, is shown in figure 28. The number of females is calculated from the average sex ratio of 1·09 males to every female which was found among the adult flies produced, while the number of eggs per female is obtained by interpolation from figure 14. The initial larvae per gram include both the species present on the meat.

The data plotted in figure 26 are essential in order to obtain the estimated potential production of eggs, since each species differs in its relationship between size of fly and fecundity (see figure 14). In figure 27 the number of flies of each species and the total fly population have been plotted against the initial mixed larval population, the whole expressed in *Lucilia* equivalents.

This method shows *C. chloropyga* to slightly better advantage than plotting actual numbers and reflects its relative success in the struggle for food more fairly. It also gives a higher total number of flies from the mixed population.



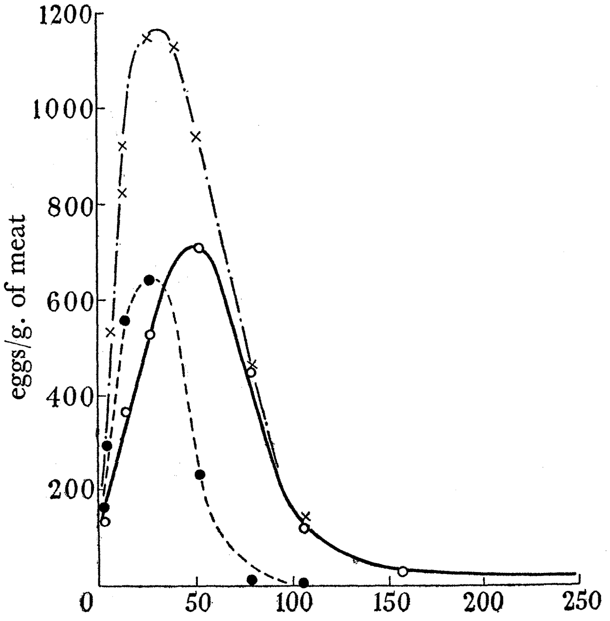


FIGURE 27.

FIGURE 28.

FIGURE 27. Resultant fly populations from mixed larval populations of *L. sericata* and *C. chloropyga* expressed in *Lucilia* equivalents. o, *L. sericata*; ●, *C. chloropyga*; ×, total flies.

FIGURE 28. Potential production of progeny from females reared from 1 g. of consumable meat in mixed populations of *L. sericata* and *C. chloropyga*. o, *L. sericata*; ●, *C. chloropyga*; ×, mean values from intraspecific experiments; —·—, total eggs in the mixed population.

If the numbers of *Lucilia* and *C. chloropyga* flies in the comparable intraspecific series are similarly treated and the means of the emergents are plotted (figure 27), a reasonably close agreement will be observed with the curve for the total flies from the mixed population. From the character of the mortality in the two populations and its close similarity to that obtained in pure cultures, this would have been expected. The comparison again emphasizes the essential similarity between inter- and intraspecific competition.

Since there is no significant difference between mixed and pure larval populations as regards size and numbers of individuals arising therefrom, it should follow that the total number of eggs which can be produced by the combined adult population from the mixed larval population will also agree with the total number from an equivalent adult population of the two species when living alone. The oviposition by *Lucilia* and *C. chloropyga* adults arising from the intraspecific series has been calculated from the mean of the two separate initial populations, the mean number of eggs produced and the *Lucilia* equivalents of the *C. chloropyga* larval populations. The resulting values have been indicated by means of crosses on the curve for total eggs from the mixed population (figure 28). The curve shows a very close fit to these points.

(iv) *Discussion.* It is evident that when *Lucilia* and *C. chloropyga* are forced to exist on the same limited mass of food, the struggle for existence resolves itself into a simple relationship. There is nothing aggressive about this sharing of the common food, and there is no evidence that the larger, more robust species (*C. chloropyga*) tends to evict the smaller species (*Lucilia*) from the meat as was noticed by Fuller (1934) in the case of *Lucilia* and *Chrysomyia* in Australia. The outcome of any shortage in this limited food supply in relation to the density of the total population subsisting upon it will depend upon the relative adaptability of the two species in their resistance to starvation. The species which can increase its growth weight the more rapidly, and attain its maximum weight in the shorter time, has the greater chance of success. Hence the ultimate advantage goes to *Lucilia.*

The given quantity of food enables a given population mass of the two species to survive and produce adults. This mass is equivalent to that produced by the same quantity of food when it is inhabited by one or the other of the two species living alone. The mean size of the individuals and the total number of eggs which they will eventually produce as a result of feeding upon the standard ration is identical in both cases. The data can therefore be related throughout to the simple common denominator of the amount of food available per individual in the initial larval population, whether it be pure *Lucilia*, pure *C. chloropyga* or a mixture of the two species.

Since the results of interspecific competition between *Lucilia* and *C. chloropyga* are merely the additive effects of intraspecific competition, interspecific competition is essentially an intensification of the struggle for food taking place in populations of single species. This intensification is caused by a greater population mass in the same environment at the same time. It is modified by the specific adaptability to adverse conditions shown by each species. Because of their difference in growth weight, a mixed population of *Lucilia* and *C. chloropyga* will not give results which are comparable with separate populations of either *Lucilia* or *C. chloropyga* which contain the same total number of larvae reared upon the same quantity of food. In the latter case, more individuals of *Lucilia* and less of *C. chloropyga* will develop than in the mixed population, although the total *mass* of individuals may be more or less the same. Because of this, it cannot be said that one species exercises any control over the total population mass of the other one.

With these two species interspecific larval competition is no more effective in the limitation of the adult fly populations than is intraspecific competition. We are left with the same problem as before, namely, the control of the total fly population arising from the carcass. It is quite certain that *C. chloropyga* does not effectively reduce *Lucilia* except to the extent by which its presence limits further the available food and space on the carcass. Even then *Lucilia* is able to forestall its rival both by its earlier appearance on the carcass and by its more rapid growth. It is thus able to exercise some measure of control over *C. chloropyga.*

It is questionable whether the terms 'struggle' and 'competition' are suitable ones for use in describing the phenomena so far studied. If, as is usually the case, they are taken to imply some sort of aggressive activity on the part of the species in acquiring food, then they are certainly not desirable in the present instance. There is no evidence that larvae of *Lucilia* and *C. chloropyga* compete for food in this sense. The simple fact is that there is often insufficient food to go round, and this arises solely through the improvident manner in which parent flies distribute their eggs.

An analogous case is seen among the slum dwellers of our great cities where the very poor produce large families in spite of the fact that food is normally scarce among such communities. It can hardly be said that children in these families 'compete' for the available food. Yet they suffer from the shortage very much in the same way as do the overcrowded progeny of the blowflies. Mortality is higher and the general size smaller than in better-fed sections of humanity.

The problem, therefore, must be regarded as one of nutritional requirements and their satisfaction or otherwise by the provisions of nature rather than in the light of a specific 'struggle'. The phenomenon which really acts as the controlling agent is, basically, sheer starvation.

If, on the other hand, we use the word 'competition' in a metaphorical sense or in that which is intended when referring to a sporting event, such as a race which goes to the swift, then it is true that *Lucilia* and *C. chloropyga* do compete for the available food. The dice are loaded only by the inherent adaptability of *Lucilia* to withstand adverse conditions.

(*b*) *Lucilia sericata* and *Chrysomyia albiceps*

According to information gleaned from periodical exposures of carcasses in the open, these two species occur together for a short period at two separate seasons of the year. These are during September to November and from April to June. During the first of these, *Lucilia* populations are disappearing from the arena very rapidly and are at a low ebb, while *C. albiceps* populations are beginning to make their first appearance. During the second period, the positions are reversed and *Lucilia* is commencing to increase in numbers rapidly while *C. albiceps* is decreasing and is already on the point of fading out. Unlike the *Lucilia-C. chloropyga* combination, in which only those two species occur together, the overlapping populations of *Lucilia* and *C. albiceps* are rarely free from the intervention of a third species. Either *C. marginalis* or *C. chloropyga* is usually present on the carcass at the same time, so that it will be on comparatively rare occasions that a straightforward competition between *Lucilia* and *C. albiceps* will take place.

Apart from the fact that these occasions do arise, we require to know the separate effects of *C. albiceps* on each of the species. This fly is the only one of the blowflies, co-existent on carcasses in South Africa, which is both predatory and cannibalistic. Its relationships will therefore differ from those of the more docile species. Some of the peculiarities arising from these habits were seen in the study of the intraspecific competition.

(i) *Mortality in the mixed population.* The data for *Lucilia* and *C. albiceps* respectively are rendered comparable with each other and with those for the same two species in the intraspecific competition series by expressing the total initial larval population and the surviving *C. albiceps* population in terms of *Lucilia.* The total mortality in the mixed population has been calculated on this basis.

The mortality in the two larval populations is plotted in figure 29. The extremely rapid increase in mortality as the initial larval density is increased, together with the exceptionally high death-rate at even the lowest densities are features of the *Lucilia* population. When more than 2000 larvae of each species are present on the given meat supply, *Lucilia* becomes eliminated. This is clearly not the effect of simple competition for the food, since the total population mass at any point is not sufficient to produce this mortality (cf. *Lucilia* and *C. chloropyga* under similar conditions). Here it is due to the predatory habits of the *C. albiceps* maggots which freely attack and destroy the *Lucilia* larvae with which they come into contact, in addition to themselves feeding upon the meat.

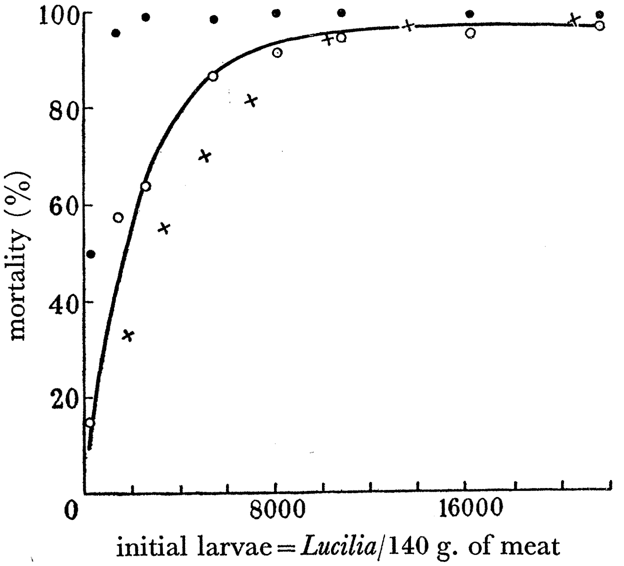
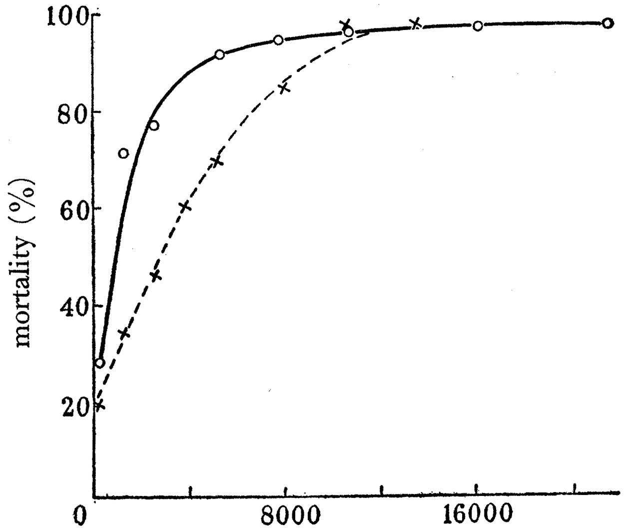


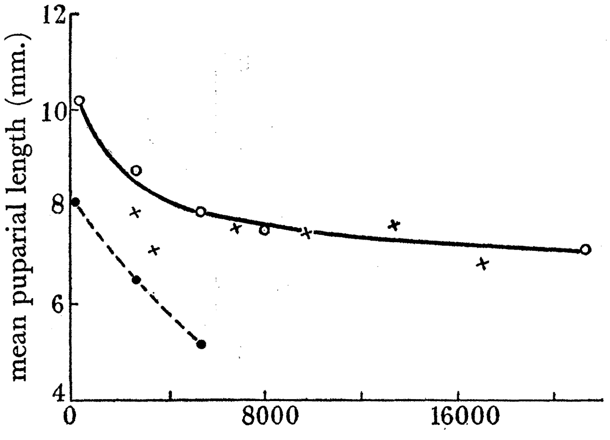
FIGURE 29. Mortality of each species in mixed larval populations of *L. sericata* and *C. albiceps*. ●, *L. sericata*; ○, *C. albiceps*; ×, *C. albiceps* in pure cultures. $y = 98(1 - e^{-0.0011x})$.

This takes place at an early stage, as is shown by comparing the mortality of *C. albiceps* in the mixed and pure cultures. In the former it is higher at the lower initial larval concentrations (i.e. up to about 9000 *Lucilia* equivalents) than in the latter. After this point, the observed values in both series fall equally well on the same curve. At the lower concentrations, more *Lucilia* are enabled to survive since the opportunities for chance encounters between larvae of the two species are reduced. Furthermore, those larvae which are eventually destroyed live longer and hence consume more food than where there is a larger population of *C. albiceps* present to attack them. Less food is therefore available for the development of the *C. albiceps* population, and there is a slightly enhanced mortality at the lower initial larval densities.

When the *Lucilia* maggots can be quickly eliminated from the culture at a very early stage of development, the *C. albiceps* mortality curve depicts what happens in intraspecific competition for food plus a certain degree of cannibalism between the *C. albiceps* larvae themselves. It will be noticed that the mortality of this species at the lowest concentration is also approximately equivalent to that at the same point in intraspecific competition. This indicates that only the usual experimental mortality takes place here. On the other hand, the *Lucilia* death-rate at the same point is about three times as great as in pure cultures.

In figure 30, the combined mortality data are plotted on the same scale as the mean of the mortality observed in pure cultures of the two species. The latter curve has been derived in the manner described for *Lucilia* and *C. chloropyga*. In contradistinction to the results observed with *Lucilia* and *C. chloropyga*, the total mortality in the mixed population of *Lucilia* and *C. albiceps* is very much higher than when comparable numbers per gram of meat of these two species are living alone, except at the higher concentrations. There will generally be a considerable reduction in the total mass and numbers of flies emerging from a carcass of given weight where these two species are associated.





initial larvae = *Lucilia*/140 g. of meat

FIGURE 30. FIGURE 31.

FIGURE 30. Total mortality in mixed populations of *L. sericata* and *C. albiceps*. ○, in mixed population; ×, mean mortality in pure cultures.

FIGURE 31. Effect of interspecific competition for food on the size of individuals in mixed populations of *L. sericata* and *C. albiceps*. ●, *L. sericata*; ○, *C. albiceps*; ×, *C. albiceps* in pure cultures. $y = 16{\cdot}63x^{-0{\cdot}08559}$.

(ii) *Reduction in size.* From the frequency distributions of puparial lengths in the surviving populations of the two species, the mean lengths of puparia in the replications of each series are plotted in figure 31, using *Lucilia* equivalents for the initial larval densities (cf. data for intraspecific competition in figure 10).

As the density of the initial mixed population of larvae is increased, *Lucilia* suffers a drastic and rapid reduction in the mean size of the surviving individuals. The size of the puparium falls to the minimum for the species at a very early stage. Even at the lowest concentration of larvae, where the *Lucilia* survival is highest, there is a marked reduction in the mean size of the individuals as compared with the relevant intraspecific series. Mortality and size reduction proceed simultaneously. It was not possible to obtain a satisfactory sample in the series containing 1000 larvae of each species. This was due to a very irregular survival in the replications. Irregularity in results appears to be peculiar to mixed populations of *C. albiceps* and other species and is probably due to the cannibalistic and predatory habits of the former.

In the case of *C. albiceps*, the same gradual decrease in general size with increasing population density took place as was observed in pure cultures of this species. The mean sizes of the individuals from pure and mixed populations are, indeed, very similar throughout (figure 31). A divergence occurs at the lower concentrations of larvae, where the individuals are somewhat larger from the mixed populations. These occur where the *Lucilia* population still produces a few survivors and where early elimination of these competitors is not so readily accomplished. At higher concentrations, where *Lucilia* can be eliminated at a very early stage, the points for *C. albiceps* from both series fall about the same curve. The predatory action of *C. albiceps* enables the maggots to obtain more food, by preying upon the *Lucilia* larvae, than can be obtained by those living in pure cultures where the effects of competition for food is more marked and where the milder effects of cannibalism cannot wholly make up for the deficit. The early elimination of *Lucilia* in a mixed population tends to nullify this advantage and the course of events substantially follows that found in a pure population of *C. albiceps*.

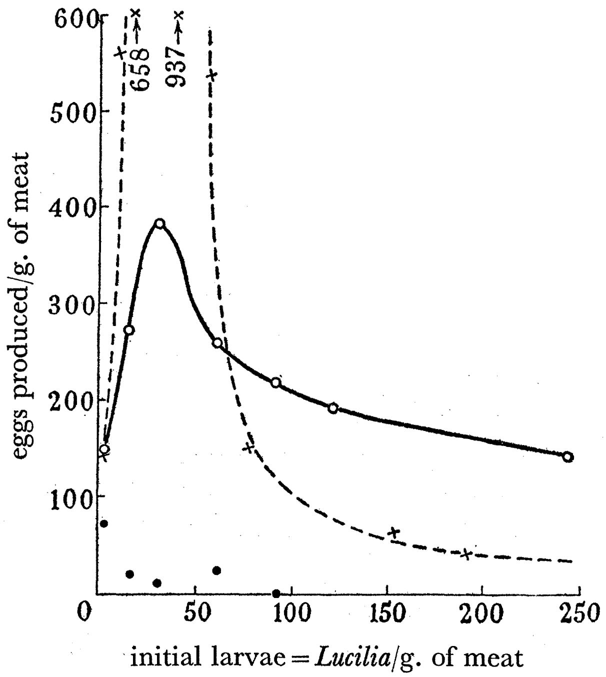


FIGURE 32. Potential production of eggs per gram of meat from mixed populations of *L. sericata* and *C. albiceps*. Symbols as in figure 31.

(iii) *Reduction in fecundity*. The outcome of the reduction in size of the *Lucilia* and *C. albiceps* individuals is very different from that obtained in mixed populations of *Lucilia* and *C. chloropyga*, even under comparable conditions.

The *Lucilia* population is severely affected by its association with *C. albiceps* in the fecundity of the surviving individuals. The egg production per gram of meat is negligible in all cases where females survive. When these two species do occur on the same carcass, *C. albiceps* exerts an efficient control over *Lucilia* and, where the initial populations are high enough, there is an elimination of the latter species, other things being equal.

The presence of *Lucilia* also has a marked effect on the co-existent *C. albiceps* population. The ultimate production of eggs per gram of meat supplied is plotted in figure 32 together with the egg production of *C. albiceps* at comparable initial larval densities in pure culture. The initial concentrations are in *Lucilia* equivalents. There is here a divergence from anything previously encountered. When the curves for *C. albiceps* in pure and mixed populations are compared, they exhibit the same general course but tell very different stories. The comparison may be divided into periods for convenience.

During the first of these an equivalent number of *C. albiceps* larvae is present initially in each series. It is indicated by the first point on the chart. There is no difference in the final population of flies or in the production of progeny, and the presence of *Lucilia* in the mixed population has not affected the issue. The second period extends to the point at which the two curves cross each other, represented by the co-ordinates of 65 larvae and 250 eggs/g. Over the range so covered, the pure culture of *C. albiceps* can produce very many more potential progeny than can be produced by the mixed populations—at the peaks of production in each case there are more than twice as many. The presence of *Lucilia* has had a detrimental effect upon the population of *C. albiceps*, in spite of becoming largely destroyed itself.

This effect is not due to any increased reduction in the general size of the individuals comprising the population—in fact, at this juncture the surviving *C. albiceps* individuals are generally larger than those produced in pure cultures—but to a reduction in the numbers of *C. albiceps* survivors. Reduction in size takes place in a normal manner and occurs concurrently with an increase in mortality as observed previously.

During the third period, where overcrowding on the medium becomes still more severe, the positions of the two curves are interchanged. With approximately 65 larvae/g. in each of the initial populations, the two series give rise to an equal number of progeny. There is a larger survival value coupled with a smaller general size in the mixed population. With further degrees of overcrowding *C. albiceps* in the mixed population produces considerably more eggs per gram of medium from the same initial population mass than does *C. albiceps* in pure culture. *Lucilia* larvae are eliminated at an early stage.

(iv) *Discussion.* There are three distinct phases in the interspecific reactions between *Lucilia* and *C. albiceps*, viz.:

(*a*) *C. albiceps* exerts some control over *Lucilia* at low concentrations of larvae on the medium. Some 28% of the population of the latter is destroyed, while *C. albiceps* is unaffected. The numbers of each species on the medium are low, and chance encounters between individuals of the two species are reduced to a minimum. Where *C. albiceps* maggots do find one of the opposite species, the latter is at once destroyed. The reduction so brought about, however, does not affect the growth of *C. albiceps*, since there is already food in sufficient quantity to serve both populations and to produce the greatest possible number of maximum-sized individuals of both. The resulting flies are comparable in size and numbers with those of a pure culture raised from the same initial population mass on the same quantity of food.

Lucilia, on the other hand, suffers a reduction in numbers, and the flies produced are not as large as those from a comparable pure culture. The progeny of these flies will be fewer and the general fly population decreases accordingly.

(*b*) With increased initial populations on the given quantity of meat, *Lucilia* is further reduced in numbers, but a few individuals survive to produce progeny. The presence of *Lucilia* now affects the populations of *C. albiceps*, as shown by an increased mortality over the comparable pure culture. This is reflected in a considerable reduction in the final capacity for egg production, due to direct competition with the *Lucilia* population for the available food. Although most of the *Lucilia* larvae are eventually encountered and destroyed by roving *C. albiceps* maggots, the latter are not yet numerous enough to accomplish this process of elimination at a stage which is early enough to prevent the consumption of an appreciable proportion of the food by *Lucilia*. In this connexion, the rapidity with which the latter can grow and utilize the food combined with the earlier period at which its most rapid growth takes place as compared with *C. albiceps* are important.

(*c*) When the initial populations become grossly overcrowded and there are sufficient individuals of *C. albiceps* present to find and destroy all the *Lucilia* maggots at a very early stage, interspecific competition for food largely disappears. The *C. albiceps* population is virtually a pure culture and would be expected to react as such. Actually, *C. albiceps* in the mixed population gave better results in the final production of progeny than when in pure culture. Thus it would seem to have gained by its association with *Lucilia*.

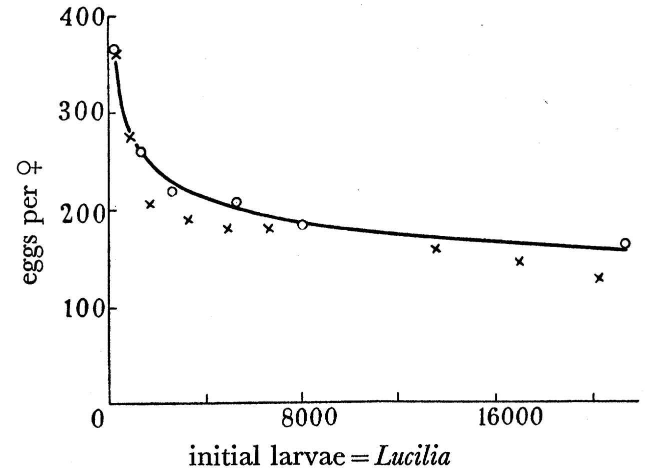


FIGURE 33. Fecundity of females of *C. albiceps* from mixed populations of *L. sericata* and *C. albiceps*. ○, *albiceps* in mixed culture; ×, *albiceps* in pure culture.

It appears that *C. albiceps* benefits from the presence of *Lucilia* in two ways:

(1) by the increase in size of individuals in the surviving population even when mortality is increased, and

(2) by the increase in number of potential progeny when large numbers of both species are present on the same piece of meat. This is difficult to account for unless some stimulation of *C. albiceps* maggots by reason of their feeding upon living matter is presumed.

The comparison in figure 32 illustrates how a blowfly species endeavours to produce the maximum number of progeny even under the most adverse conditions. The total number of eggs produced per gram of meat by *C. albiceps* in mixed populations can be duplicated in the series of pure cultures, but, in order to do this, it is necessary to select initial population masses in the pure cultures which are much lower than those in the mixed populations. Thus, if the final point in the mixed series is chosen, i.e. at an initial population density equivalent to 244·5 *Lucilia* larvae/g., the same number of eggs produced per gram in pure culture will be found corresponding to the ordinate of 154·25 *Lucilia* equivalents/g. In the former population, there is the *Lucilia* equivalent of 154·25 *C. albiceps* larvae/g., so that the initial population is nearly double that of the corresponding pure culture. The survivals in the mixed and pure populations were 2·05 and, approximately, 1·8 flies, or 0·88 and 0·76 females, per gram respectively. These are again roughly in the same proportions as were the initial populations.

The puparial lengths were 7·12 and (by interpolation) 7·59 mm. respectively. The females of these surviving populations would be capable of laying 160 and 190 eggs each, giving a total of 141 and 144 eggs/g. of medium respectively. Hence, in the mixed population at the higher initial population mass there was a higher survival value but a general reduction in size as compared with the pure cultures. Both succeeded in producing the same number of eggs by means of different adjustments to the situation. A similar relationship will be found at other points on the two curves.

(*c*) *Chrysomyia albiceps* and *C. chloropyga*

Populations of these two species on carcasses in the field overlap from September to November and again from May to June. During the former period, *C. albiceps* is gradually increasing in numbers while *C. chloropyga* populations are decreasing. It is possible that the final sharp decline in *C. chloropyga* is due to the presence of *C. albiceps* in some measure, but there is no convincing evidence that this is the case from the field records. Probably it is a contributory cause. During the second period of overlap, the *C. albiceps* population is on the decline and is at a fairly low ebb, while the *C. chloropyga* population reaches its peak at this time. The presence of *C. albiceps* seems to have no appreciable effect, although it is possible that *C. chloropyga* is prevented thereby from increasing still more rapidly than is actually the case at this time.

Data obtained from field exposures of carcasses, which represent the end-results of any competition or other interaction taking place between co-existent populations of fly larvae, give no definite clue to the events taking place in the mixed population. Thus, from the above account which has been drawn up from a study of the charted results of observations in the Karroo region, it is not possible to say whether *C. albiceps* has or has not any appreciable effect upon populations of *C. chloropyga* during those periods in which the two species exist together on the carcass. Similarly, the relationship between *Lucilia* and *C. albiceps* is not clearly demonstrated. It is only by the more detailed studies which can be made under controlled conditions that an answer to this problem can be satisfactorily obtained.

The opportunities for any interaction between *C. albiceps* and *C. chloropyga* occur more frequently than in the case of *Lucilia* and *C. albiceps*. With the first two species, the overlapping periods of occurrence take place at a higher larval population density than with the last two species.

(i) *Mortality in the mixed population.* For comparative purposes, the initial mixed larval population and the surviving populations of each species were expressed in *Lucilia* equivalents. The total surviving population was obtained in terms of *Lucilia*, and the total mortality in the mixed population calculated on this basis. The mortality data are plotted in figure 34.

The mortality for *C. chloropyga* is strongly reminiscent of that in populations of *L. sericata* under similar conditions. The same rapid efficient control by larvae of *C. albiceps* is evinced, although *C. chloropyga* would appear to be able to survive slightly more successfully than *Lucilia*, probably because of its larger size. There is a complete destruction of *C. chloropyga* larvae at a density of approximately 10,000 *Lucilia* equivalents/140 g. of meat in the mixed population. This effect is due to the predatory action of *C. albiceps*, and the result is substantially the same as in the case of the *Lucilia-C. albiceps* populations. On the same chart, the observed values for mortality in comparable pure cultures of *C. albiceps* are plotted by means of crosses. It will be noticed that, while some *C. chloropyga* in the mixed population survive, the mortality in the *C. albiceps* population is higher than when this species exists alone. As soon as the elimination of *C. chloropyga* is achieved and only *C. albiceps* is left, the mortality in the two series is the same.

As in the *Lucilia-C. albiceps* combination, this would appear to be due to the longer survival of *C. chloropyga* at the lower initial population densities and hence to a greater use of the available food by this species. This has the effect of depriving the *C. albiceps* population of its full quota. This shortage is apparently not balanced by the nutriment obtained by *C. albiceps* larvae through their predacious habits. As the total mixed population is increased in numbers, the *C. chloropyga* larvae are destroyed at an earlier stage and the mortality of *C. albiceps* more and more approximates to that in pure cultures until, finally, agreement is reached when *C. chloropyga* is completely and quickly destroyed at the higher concentrations.

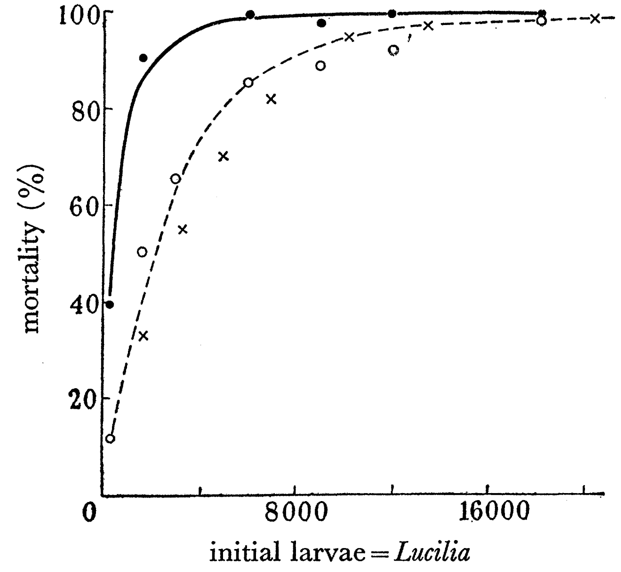


FIGURE 34. Mortality of each species in mixed populations of *C. chloropyga* and *C. albiceps*. ○, *C. albiceps*; ●, *C. chloropyga*; ×, *albiceps* in pure cultures. $y = 99(1 - e^{-0{\cdot}0009824x})$.

A certain proportion of the food ingested by the *C. chloropyga* larvae is used up in the formation of organs and structures which cannot be ingested, in their turn, by the predacious *C. albiceps* maggots. By this means, some of the consumable food supplied is rendered permanently unattainable by the *C. albiceps* population. The proportion will depend upon the number of *C. chloropyga* larvae surviving and upon the length of time during which those which eventually succumb are allowed to go on feeding. It is highest where the greatest number of *C. chloropyga* is able to survive or where they are able to survive the longest, i.e. at low initial populations; it is lowest where the *C. chloropyga* larvae are destroyed at an early stage of the mixed population, i.e. at high initial densities.

In so far as it is governed by the quantity of available food, the mortality in the *C. albiceps* population will reflect this factor and will show an increase over that in pure cultures. It is noteworthy that this increase is more marked in the *Lucilia-C. albiceps* combination, where

C. albiceps is associated with a smaller companion requiring less food for its indigestible structures but which feeds more rapidly.

In figure 35, the total mortality for the mixed population is plotted. For comparison, the mean of the mortalities in the series of pure cultures of the same two species is plotted to the same scale. Up to an initial population of approximately 10,000 *Lucilia* equivalents the mortality in the mixed population is considerably higher than is the mean mortality of the pure cultures. This is directly due to the higher mortality of *C. chloropyga* which is brought about by the aggressive action of *C. albiceps*. At and beyond this point, the two curves approximately coincide, since the mortality in both cases is practically that of a pure culture of *C. albiceps*.

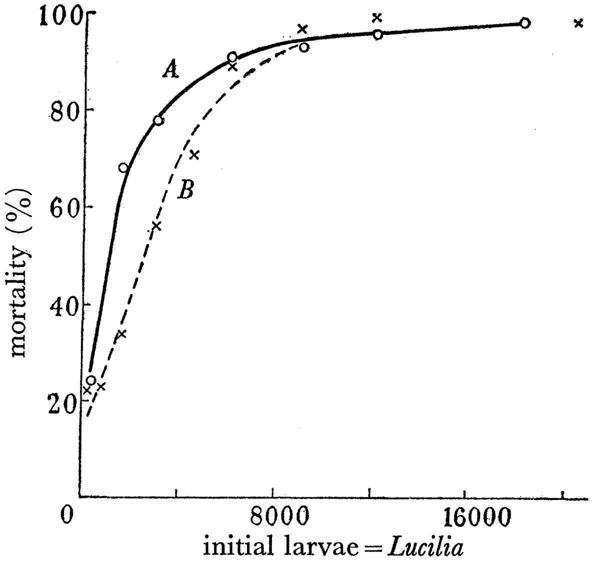


FIGURE 35. Total mortality in mixed populations of *C. albiceps* and *C. chloropyga*. ○, in mixed population; ×, mean mortality in pure cultures. A: $y = \frac{x}{10 + 0{\cdot}0095x}$.

There are thus two distinct phases corresponding to the degree of infestation of the available food. At the higher initial larval populations in mixed cultures, *C. chloropyga* is very quickly eliminated before it has had time to influence appreciably the quantity of medium available. After this point, the struggle for food is essentially an intraspecific one between larvae of *C. albiceps*. At lower concentrations, *C. chloropyga* is also able to compete.

A comparison between the total mortality shown in figure 35 and that for the mixed populations of *Lucilia* and *C. albiceps* in figure 30 shows an essential similarity. The mortality in the *C. albiceps*-*C. chloropyga* population is slightly lower in the intermediate series because of the more rapid elimination of the competing *Lucilia* in the *Lucilia*-*C. albiceps* series at these points. The general course of events, however, is fundamentally the same in both instances.

(ii) *Reduction in size.* Frequency distributions of the puparial lengths of the surviving populations of larvae of the two species when in mixed populations were made. As in the case of the *Lucilia*-*C. albiceps* association, the species which is attacked exhibits some degree of irregularity in the samples taken for this analysis. The records obtained are therefore not as satisfactory as those resulting from similar samples from pure cultures or from populations of the predatory species in mixed populations. The mean puparial lengths for each series are plotted in figure 36.

The similarity in form of the curves obtained to those for the intraspecific series of the same two species is marked (cf. figure 10). The data in both instances can be fitted most satisfactorily by equations of the same general form. The rapid decrease in size of *C. chloropyga* individuals as the total population is increased is paralleled by that experienced by *Lucilia* larvae when in association with *C. albiceps*. This decrease in size takes place in spite of the reduction in population arising from mortality due to the predatory activities of *C. albiceps*. The contention of Fuller (1934, p. 47) that the presence of a predatory species results in fewer but larger adults emerging does not hold in the case of *C. albiceps* and its competitors. Fewer adults are produced, but these gradually tend towards the smallest possible size for the species and are always smaller than those produced from comparable pure cultures.

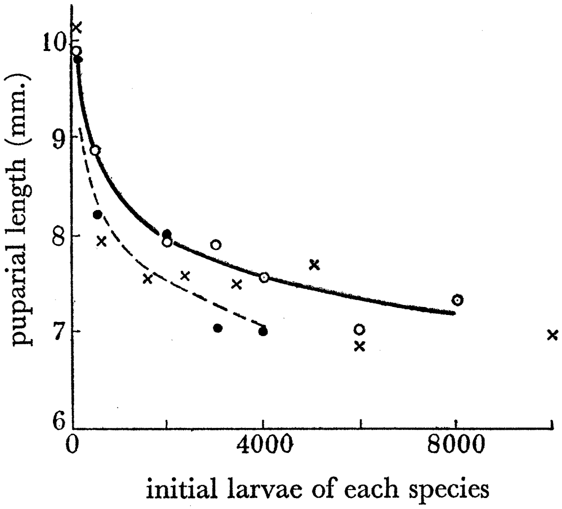


Figure 36. Reduction in size of individuals in mixed populations of *C. albiceps* and *C. chloropyga*. ○, *C. albiceps*; ●, *C. chloropyga*; ×, *albiceps* in pure cultures.

The effect of interspecific competition and its co-existent predatorism on the size of individuals in the *C. albiceps* population exhibits features which are very similar to those observed in the *Lucilia-C. albiceps* populations. At first there is the same increase in the mean size of *C. albiceps* puparia over that attained in pure cultures in which comparable numbers per unit of food were used. This is followed by approximate agreement between the two different series when the initial population density is high, i.e. over 4000 larvae of each species (see figure 36). Again, *C. albiceps* apparently gains by its association with a competitor; but when it can and does eliminate this competition for food at an early stage, this gain disappears and the population of *C. albiceps* assumes the attributes of a pure culture.

(iii) *Reduction in fecundity*. In figure 37 the total potential number of eggs which can be produced by the flies emerging from each gram of meat is plotted against the initial larval population per gram expressed in *Lucilia* equivalents.

The rapid rise in egg production, followed by the gradual decline in the *C. albiceps* population as the initial larval density increases contrasts with the continuous decline which *C. chloropyga* exhibits from the start. The latter species is evidently not as quickly or severely affected as is *Lucilia* under similar circumstances, but it is completely suppressed at a comparatively low initial larval density. The maximum production of eggs by the surviving population of *C. albiceps* is somewhat lower than that attained when this species is associated with *Lucilia*. This is probably due to the slower destruction of *C. chloropyga* larvae at those population densities at which maximum egg production is possible. This, coupled with the larger size of *C. chloropyga* and the somewhat larger surviving population of this species, tend to render a greater amount of food unavailable to the *C. albiceps* larvae. This no doubt contributes largely to the difference in shape of the *C. albiceps* curve in figure 37 (cf. figure 32).

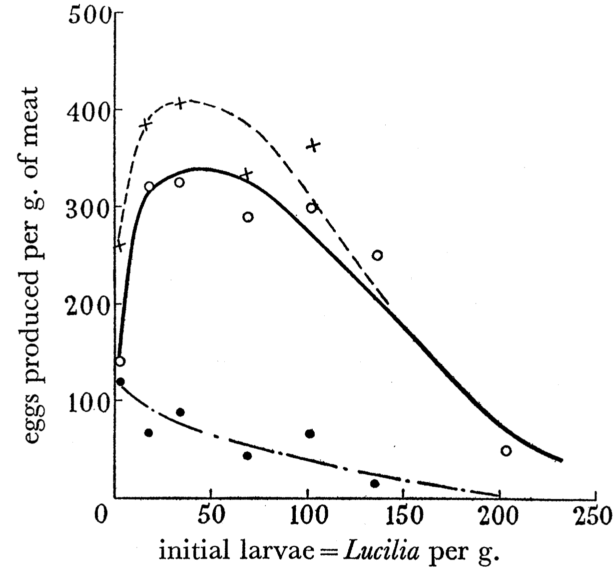


FIGURE 37. Potential production of eggs per gram of meat from mixed populations of *C. albiceps* and *C. chloropyga*. ○, *C. albiceps*; ●, *C. chloropyga*; ×, total eggs.

The individuals among the *C. chloropyga* population which survives maintain a reasonably good size, although they are very much smaller than when developed in comparable pure populations. On the other hand, *Lucilia*, when in conjunction with *C. albiceps*, is unable to do so (see figure 31). Although populations of *C. chloropyga* experience a heavy mortality at all densities in mixed populations, the survivors are more successful in obtaining food for themselves than where a straight competition with *Lucilia* larvae takes place (cf. figure 25). It would seem that the predatory species, by reducing the population of *C. chloropyga* rapidly and efficiently, has reduced the degree of total competition for food within the mixed population. The survivors therefore tend to be larger than is the case where simple interspecific competition takes place although not larger than those surviving intraspecific competition.

(iv) *Discussion.* A comparison of the present series with that for mixed populations of *Lucilia* and *C. albiceps* shows that the general relationships between the predatory and non-predatory species are fundamentally the same. Although the more robust *C. chloropyga* larvae are able to withstand the onslaught of *C. albiceps* more successfully, they are nevertheless quickly and efficiently suppressed in much the same way as are *Lucilia* populations. On the other hand, the maximum production of *C. albiceps* is also depressed, as was the case in the *Lucilia*-*C. albiceps* populations. This is seen by comparison with the series of pure cultures of *C. albiceps*. At the higher initial densities, *C. albiceps* again benefits from its association with a non-predatory species, and the potential production of eggs from each gram of the medium remains generally above that attained in pure cultures. Reasons for this have been suggested.

The extent of the control of *C. chloropyga* by *C. albiceps* will depend, among other things, upon the relative densities of the two populations and upon the total initial density of the mixed population per unit quantity of consumable food. The actual mechanism of this control is twofold. The two populations compete for the available food and thus produce an effect comparable to intraspecific competition, as was observed in the *Lucilia-C. chloropyga* populations; and *C. albiceps* actively destroys the *C. chloropyga* population. This influences the degree of competition for food which exists between the rival populations and is to the benefit of *C. albiceps*. Predatorism is the main factor in the control of *C. chloropyga*.

The value of *C. albiceps* in the general control of *C. chloropyga* populations in the field is limited by the frequency with which these two species occur at the same time of the year on carrion. This is similar to the position shown by *Lucilia* and *C. albiceps*. Furthermore, when the populations of these species are known to overlap, the total population of their larvae on the carcass is comparatively small. The intensity of competition between the two species will consequently be at a minimum at these times, as will also the effect of the carnivorous propensities of *C. albiceps*. It is unlikely, therefore, that *C. albiceps* forms a major factor limiting the *C. chloropyga* population in nature, although it may be an important contributory cause of a more rapid decline in the latter than would otherwise be the case.

3. *Competition between three species* (Lucilia sericata, Chrysomyia albiceps *and* C. chloropyga)

According to data obtained from carcass exposures, it is on comparatively rare occasions that more than two species occur together in any numbers on the same carcass. During certain periods of the year, however, there are more than two. During May, the following populations overlap: *L. sericata, C. chloropyga, C. albiceps and C. marginalis*. Of these, *Lucilia* is the only one which increases its general population to any extent after this fourfold competition has taken place. During November, *C. chloropyga*, *C. albiceps* and *C. marginalis* occur together. *C. marginalis* then increases in numbers while *C. albiceps* decreases in December and then shoots up to a peak in January when *C. marginalis*, in turn, falls off. After November, *C. chloropyga* is no longer obtained from carcasses. A very small population of *Lucilia* may or may not be present in November. The overlapping periods given here are marked by a comparatively low surviving population of each of the species concerned and would seem to coincide with the times of least abundance among the parent adults.

It must be emphasized that this information is derived from the end-results of carcass exposures, i.e. from the records of the flies obtained therefrom. While these give an indication of the relative abundance of species at different times of the year, they do not indicate the absolute presence or absence of any one species at any given time. The data refer to the populations after they have survived competition and other vicissitudes on the carcass, and some initial populations may perish entirely and so leave no trace of their presence. For example, there are probably occasions on which *Lucilia* deposit eggs on a carcass when no adults result, complete mortality having occurred. This may happen when *C. albiceps* is in the ascendancy.

The periods during which the main populations are involved together on the carcass are, however, somewhat limited and are apparently largely determined by seasonal fluctuations in the species concerned. It seems that when the Lucilias are at their peaks of abundance, few, if any, flies of *C. albiceps* oviposit on the same carrion.

(i) *Mortality in the mixed population.* Curves for the mortality in each of the three populations are shown in figure 38. These should be compared with those for the *Lucilia-C. chloropyga*, *Lucilia-C. albiceps*, and *C. albiceps-C. chloropyga* mixed populations (figures 24, 29 and 34) as well as with those for mortality under conditions of intraspecific competition for food (figures 16 to 18). The necessary adjustments for initial density must be made in each case.

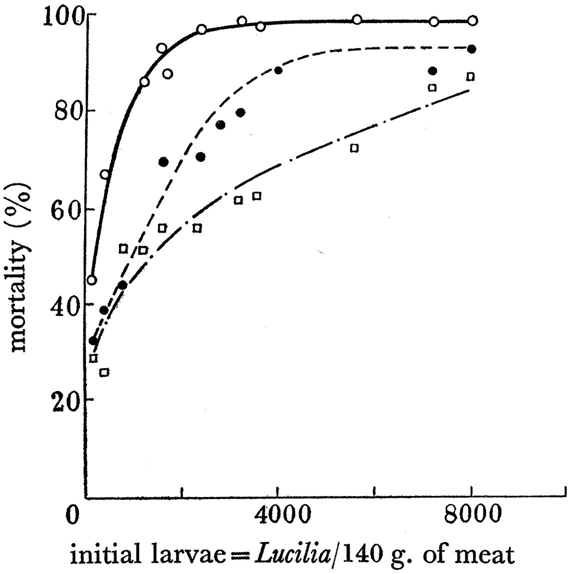


FIGURE 38. Mortality of each species in mixed larval populations of *L. sericata*, *C. chloropyga* and *C. albiceps*. ○, *L. sericata*; ●, *C. chloropyga*; □, *C. albiceps*.

It is clear that *C. albiceps* is not affected by the presence of the third species, whether it be *C. chloropyga* or *Lucilia*. The proportion of its population which succumbs during threefold competition is much the same as that when this species is associated with only one other fly. *Lucilia* is eliminated with practically the same rapidity as in the *Lucilia-C. albiceps* populations. The most striking difference between the present and previous series is in the *C. chloropyga* population. This suffers a lower percentage mortality in the threefold population than when with *C. albiceps* alone but a higher one than when with *Lucilia* alone. The curve falls approximately midway between those for the twofold series. Only at the higher initial concentrations do all the values for *C. chloropyga* mortality in the various series coincide. This is roughly at the point where there is complete mortality of this species when in pure cultures.

Thus *C. chloropyga* has benefited to some extent by the presence of *Lucilia*. The most reasonable explanation of this is that the less robust and smaller *Lucilia* larvae are more easily attacked and destroyed than are the larger *C. chloropyga* larvae, and that this serves in some measure to reduce the total destruction of the latter by *C. albiceps*. The situation, however, is complicated. Not only is the predacious habit of *C. albiceps* a factor in the association, but both intra- and interspecific competition for food enter into the picture.

It is possible to offer a further partial explanation for the smaller *C. chloropyga* mortality in the threefold competition.

Interspecific competition between *Lucilia* and *C. chloropyga*, while not actually controlling the total population mass produced per unit of food, yet reduces the number of survivors in each of the populations. In the threefold population this reduction must also occur to some extent and at a fairly early stage. There are thus fewer *C. chloropyga* individuals than in the comparable series of the *C. albiceps-C. chloropyga* series. The chances of the *C. albiceps* larvae encountering *C. chloropyga* maggots are greatly reduced, and hence the proportion of the latter which is found and destroyed will be much smaller. The same reasoning will apply in the case of *Lucilia* and there is a slight tendency for the mortality to be lower than in the *Lucilia-C. albiceps* populations at the lower initial densities. The explanation is not satisfactory when taken by itself but must be regarded as contributory to the main issue.

If the present series is compared with others at the same initial densities as are used in the curves, allowance must be made for the presence of three species in the mixed population instead of only one or two. The number of *C. chloropyga* larvae in the initial populations of the threefold series will be much smaller than that in comparable series of *C. albiceps-C. chloropyga* or *Lucilia-C. chloropyga* populations. This in itself considerably lowers the number of chance encounters between *C. chloropyga* and *C. albiceps* in the threefold population as compared with the *C. albiceps-C. chloropyga* series. A smaller proportion of the *C. chloropyga* population is found and destroyed. Again, this is only a partial explanation and must be combined with the greater difficulty of attack as compared with *Lucilia* and with other factors.

The curve for combined mortality in mixed populations is similar in form to that for the mean mortalities in series of pure cultures (see figure 39). The two curves run almost parallel throughout, with that for combined mortality consistently higher than the curve for pure cultures. This difference must be attributed mainly to the destruction of competing larvae by *C. albiceps*. A control of up to 40 % of the total population mass is produced by this means. The value of a predatory species as opposed to straightforward competition for food between species in the control of the general population of flies is clearly demonstrated both by this comparison and by comparing these curves with that for the combined mortality in the *Lucilia-C. chloropyga* populations.

(ii) *Reduction in size.* The numbers of surviving *Lucilia* and *C. chloropyga* in the mixed populations were so low and variable that satisfactory samples on which to base frequency distributions of puparial lengths were seldom obtained. Because of this, the whole of the pupal population was taken and measured in each case and the means of these measurements are used (figure 40) to illustrate the effect of the association of species on the size of the individuals.

Reduction in size of the surviving *Lucilia* population takes place more gradually than when this species occurs with *C. albiceps* alone, although more rapid than when in pure culture or in association with *C. chloropyga*. There is a reduction in the size of *C. chloropyga* individuals as compared with the relevant *C. albiceps-C. chloropyga* populations. This is especially marked at the lower initial population densities. It is no doubt due to the presence of the more rapidly feeding *Lucilia* larvae. On the other hand, *C. albiceps* benefits by the association where the amount of food per larva is highest and where any deficiency can be made good by preying upon the *Lucilia* population. At higher concentrations, the size attained by the larvae is less than that at comparable densities in the twofold populations (cf. figure 31). Here the amount of food per larva is small and *C. albiceps* is unable to compensate itself for this before the *Lucilia* and *C. chloropyga* populations have rendered a considerable proportion of it unavailable. The presence of the rapidly feeding *Lucilia* population has a distinct bearing on this (cf. figures 31, 36 and 40). On the whole the reduction in size of *C. albiceps* is not serious in comparison with that in the populations of the other two species, since this is largely compensated for by the lower mortality. It should be able to maintain its general population at a higher level than either *Lucilia* or *C. chloropyga* when the three species occur together.

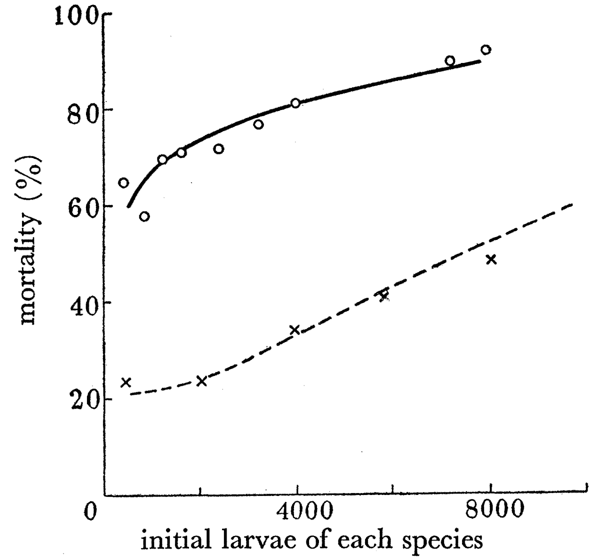


FIGURE 39.

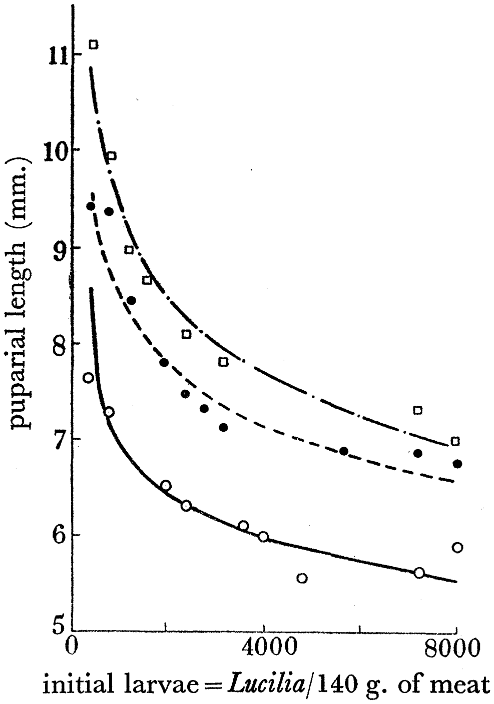


FIGURE 40.

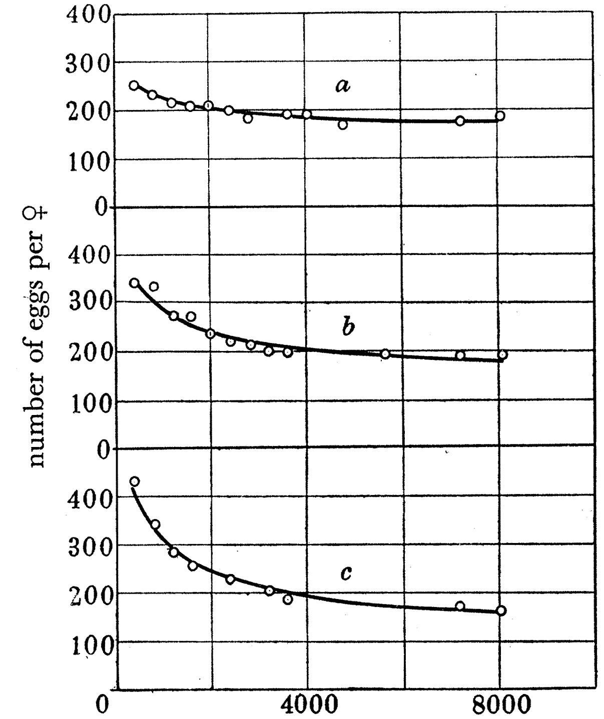
FIGURE 39. Total mortality in mixed populations of *L. sericata*, *C. chloropyga* and *C. albiceps*. ○, in mixed population; ×, mean of pure cultures.

FIGURE 40. Reduction in size of individuals with increasing larval density in mixed populations of *L. sericata*, *C. chloropyga* and *C. albiceps*. ○, *L. sericata*; ●, *C. chloropyga*; □, *C. albiceps*.

(iii) *Reduction in fecundity*. The effect of the association on the number of eggs which can be laid by each surviving female at the first oviposition is shown in figure 41.

Lucilia flies are the least affected, while *C. albiceps* suffers most, with *C. chloropyga* occupying the intermediate position. Thus, at the higher initial concentrations, the few surviving *Lucilia* are able to produce more eggs per female than are *C. albiceps* females. Even when the mortality is at its highest, *Lucilia* is able to produce sufficient eggs to maintain a future population on a fresh supply of food. The position with regard to *C. chloropyga* is similar.

Figure 42 illustrates the potential production of progeny by each of the three species. The probable oviposition by the surviving *C. albiceps* follows a reasonably normal trend, increasing with increase of initial population density to a maximum and then decreasing fairly gradually as the larval density becomes higher. On the other hand, *Lucilia* exhibits a somewhat rapid but regular decline in egg production until a lower limit for the series used is reached. Since the survival of *Lucilia* is consistently low throughout the series, this curve and that for the number of eggs per female tend to approximate, for the total production of eggs per gram is never much more than that of a single female.



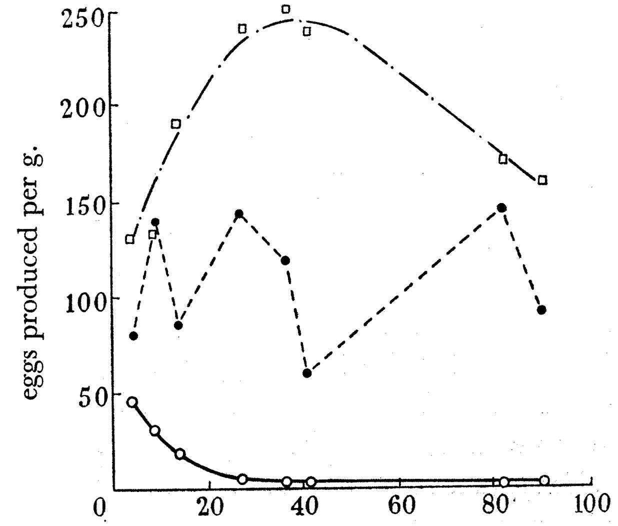


FIGURE 41. FIGURE 42.

FIGURE 41. Fecundity of females emerging from mixed populations of *L. sericata*, *C. chloropyga* and *C. albiceps*. *a*, *L. sericata*, $y = 466{\cdot}8x^{-0{\cdot}1339}$; *b*, *C. chloropyga*, $y = 1032x^{-0{\cdot}233866}$; *c*, *C. albiceps*, $y = 1914x^{-0{\cdot}33399}$.

FIGURE 42. Potential production of eggs per gram of meat in mixed populations of *L. sericata*, *C. chloropyga* and *C. albiceps*. Symbols as in figure 40.

The most striking feature is the marked irregularity of the potential oviposition of *C. chloropyga*. No smoothed curve can be drawn to fit the data. It is governed by irregular survival values and not by any marked variation in the size of the individuals in the different series. The small numbers of individuals in the samples obtained in the different populations and the direct effect of the presence of a predatory and non-predatory species on the medium are contributing factors. The interactions between the predatory species, the *C. chloropyga* population and that of a more easily attacked non-predatory species might tend to produce irregularity in the numbers of surviving individuals and in the size of the survivors. The most that can be said of the *C. chloropyga* egg production at this stage is that it is intermediate between that of the other two species.

When the above data are taken as representing the probable future generations of the three species, the control obtained at the population densities used in the series is not satisfactory from a practical point of view. Although the mortality produced in populations of *Lucilia* and *C. chloropyga* by their association with the predatory *C. albiceps* was high and the reduction in size of the individuals was considerable, the high fecundity of the surviving adults makes a rapid recovery in the succeeding generation possible. This is particularly so with *Lucilia*, which is less influenced by the size factor than are the others.

That the general population of flies can effect such a recovery is amply illustrated by taking the lowest values for *Lucilia* in the present series. When the highest initial population is present, at least two eggs are produced from each gram of consumable food. Assuming that an average sheep carcass contains approximately 16 kg. of consumable meat, the *Lucilia* population surviving from a similarly constituted mixed population on a carcass of this size would produce approximately 32,000 eggs. This is sufficient to provide for a rapid increase in the general abundance of the species if the necessary fresh food supply is available and if *C. albiceps* is no longer present to provide a check.

(iv) *Discussion.* The effect of true competition for the common food supply is very largely masked by the increased mortality in the *Lucilia* and *C. chloropyga* populations resulting from attack by *C. albiceps*. It becomes evident only when *C. albiceps* exhibits a general decrease in mean size as a result of removal of available food by the feeding of the remaining two species prior to their destruction by *C. albiceps* larvae.

The situation in the threefold population is much as follows. At the beginning, all three species are small in size and are primarily concerned in what is practically a straightforward competition for the food supply. They are mainly engaged in absorbing and therefore removing food in a manner governed by their respective normal growth characteristics. At the same time, a certain proportion of the individuals in the populations of *Lucilia* and *C. chloropyga* is removed from the picture through destruction by *C. albiceps*. This proportion will depend upon the relative numbers on the medium but will generally be comparatively small at this stage. The removal of individuals, however, tends to decrease the intra- and interspecific competition and the position for the survivors is improved up to a point.

The reduction takes place progressively in the history of each mixed population. As the *C. albiceps* larvae become larger and as the food supply dwindles, they tend to rove about more freely and are more and more likely to encounter individuals of other species. Destruction of the latter tends to increase in intensity as the mixed population becomes older.

The more rapid this destruction, the more successful will the *C. albiceps* population be, both in its survival and in the general size of its individuals. But this destruction is accomplished best when the initial density is high, since it is then that the larger *C. albiceps* population is afforded more opportunities for encountering larvae of other species. This is counterbalanced to some extent because the larger the initial population, the more it will suffer from intense intraspecific competition and, in the case of *C. albiceps*, the more will the cannibalistic propensity become evident. The latter habit will also tend to reduce the degree of intraspecific competition during the later stages.

The situation is therefore not simple. It seems evident, however, that the end-factor which will serve as the main limit to the degree of survival and size of individuals in *C. albiceps* populations is straightforward intraspecific competition.

In mixed populations there is thus a succession of events or phases which may be summarized as follows:

(1) Intra- and interspecific competition for the available food supply predominates and rapidly reduces the amount of food which is available during the later stages. This is combined with a certain degree of destruction of other species by *C. albiceps* which is not yet serious.

(2) Destruction of *Lucilia* and *C. chloropyga* maggots increases and predominates, reducing the degree of interspecific competition between the three species and the intraspecific competition between *Lucilia* and *C. chloropyga.* During this phase, *C. albiceps* larvae become compensated in some measure for the depleted food supply.

(3) The only species present in any appreciable numbers is *C. albiceps.* Competition between it and the other species is practically eliminated. The predominating feature is now the intraspecific competition between *C. albiceps* larvae. This is modified to some extent by their cannibalistic habit which increases as the intensity of competition increases and which removes individuals from the population so that those surviving obtain more food and are able to mature.

As far as the control of *Lucilia* and *C. chloropyga* populations is concerned, phase 2 above is the important one. During this period a drastic reduction takes place as a direct result of attack by *C. albiceps* and not of competition in the true sense.

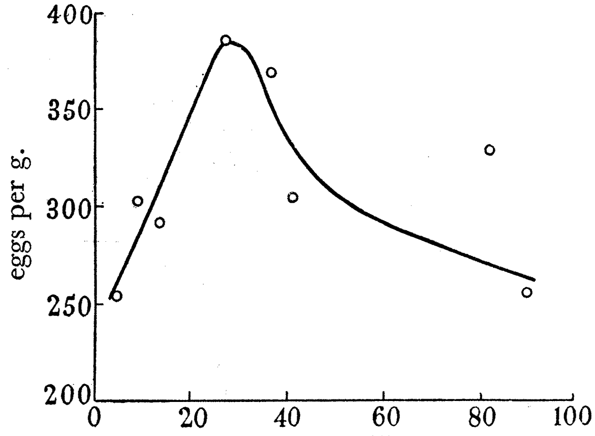


FIGURE 43. Total production of eggs per gram of meat from mixed populations of *L. sericata*, *C. chloropyga* and *C. albiceps.*

VII. SOME FACTS CONCERNING *CHRYSOMYIA MARGINALIS*

It was not possible to conduct experiments with *C. marginalis* on the extended scale used with the other species. Because of this, the data available for *C. marginalis* were not considered when these flies were discussed. Before examining the practical aspects of the results obtained, it seems worth while to give the facts that are known. These throw some light on the role that is played by *C. marginalis* on the carcass. To do this is the more desirable, since this species has been chosen, on very flimsy evidence, as the main factor controlling populations of primary flies on carrion in the field (see Hepburn 1943 *b*, Mönnig 1942, Mönnig & Cilliers 1944). Furthermore, recommendations for control measures which involve special treatment of carcasses have been based upon this opinion (Mönnig 1942).

The extreme irregularity of oviposition by this fly in captivity proved a severe handicap to experimental treatment. This irregularity appears to be due to the somewhat limited range of atmospheric and other conditions which induce abundant egg-laying by this species. Humidity was one of the most important of these conditions, and no eggs were obtained in the laboratory until the relative humidity of the atmosphere in the breeding room had been raised to nearly 90%. Although other workers in South Africa have maintained that *C. marginalis* oviposits on very fresh carcasses, this is not supported by laboratory experience. Fresh meat is apparently not as acceptable as meat which is some hours older than that utilized by *Lucilia*, *C. albiceps* or *C. chloropyga.*

In spite of the difficulties encountered, some definite statements can be made and some tentative conclusions drawn which are in direct conflict with those which have previously appeared in print.

1. *The normal growth of* Chrysomyia marginalis *larvae*

Following the general technique and methods outlined for the other blowfly species, the normal growth of *C. marginalis* larvae in pure culture was determined by taking records of growth weights at intervals until the larvae pupated. Ample food was provided during the growing period. The cultures were kept at a temperature of 80° F throughout. The results are plotted in figure 44. From this the following significant data are derived, which should be compared with those for *Lucilia* and the other species (cf. table 1).

maximum growth weight per 100 larvae (g.)	time attained (hr.)	period of most rapid growth (hr.)	increment (g.) per 100 larvae per hr.
11·36	131	70–110	0·0867

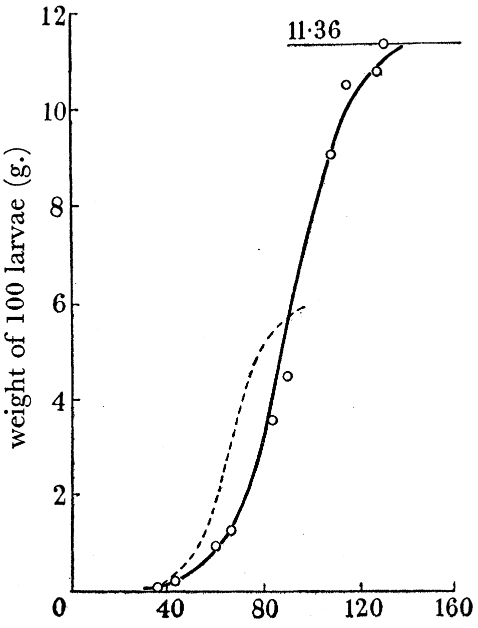


FIGURE 44. *C. marginalis*: Normal growth of larvae on meat in pure culture at 80° F.

$$y = 0{\cdot}0153 + \frac{11{\cdot}3472}{1 + e^{7{\cdot}36832 - 0{\cdot}08013t}}$$

The following points will be noted:

(1) The total growth period of *C. marginalis* is longer than that of any of the other species under the same conditions. It is 13 hr. longer than that of *C. chloropyga*, 22 hr. longer than that of *C. albiceps* and 40 hr. longer than that of *Lucilia*. Each of these species therefore has a distinct advantage over *C. marginalis* in interspecific competition for food.

(2) The period of most rapid growth in *C. marginalis* occurs at a later stage than in any of the other species, namely, 6 hr. after *C. albiceps*, 10 hr. after *C. chloropyga* and 20 hr. after *Lucilia*. This adds to the disadvantage in (1) above.

(3) In the increment of growth weight/hr., *C. marginalis* is higher than *C. chloropyga* or *Lucilia* (1·29 and 1·34 times as great respectively) but is lower than *C. albiceps*. This advantage over the two first-named species is offset by the disadvantages stated above, since the increment is spread over the total growing period and is greatest during the most rapid growth period which occurs much later than in *Lucilia* and *C. chloropyga*.

Since it is especially in relation to the control of *Lucilia* populations that *C. marginalis* has been brought to the fore, comparisons with *Lucilia* will be stressed here. In order to do this more readily, the *Lucilia* growth curve has been superimposed upon that for *C. marginalis* in figure 44.

Lucilia is half-way through its most rapid growth period by the time that *C. marginalis* enters this phase. In fact, by this time, *Lucilia* has completed nearly three-quarters of its total growth and has a very excellent chance of finishing it before a shortage of food occurs. Furthermore, *Lucilia* can, at this juncture, form viable pupae, larvae which have attained this weight having given rise to healthy adults in experiments. The relative weights of the larvae of the two species at this point are significant. While *Lucilia* larvae weigh 0·380 g. each, *C. marginalis* are only 0·0160 g., i.e. less than half the size of *Lucilia*. There can therefore be no question of any crowding out of *Lucilia* by *C. marginalis* when the two species find themselves in competition for a common food supply of given size, presuming that the larvae hatched at approximately the same time. It is only after 90 hr. of feeding that the *C. marginalis* larvae attain to approximately the same size as the *Lucilia* larvae at one and the same time. At this stage, however, the latter species has nearly completed its full growth, while *C. marginalis* is only half-grown.

There is a big disparity in size between the fully grown larvae of the two species. That of *C. marginalis* is nearly double that of *Lucilia*. On a given limited food supply, *Lucilia* should therefore be able to produce nearly twice the population that can be produced by *C. marginalis*. In other words, overcrowding and severe intraspecific competition for food will occur at a much lower initial population density in the case of *C. marginalis*.

The account which follows is based upon incomplete series of trials and is not calculated to give more than a general indication of the results to be expected when larvae of *C. marginalis* compete for food either among themselves or with other species. The information obtained so far will suffice to explode certain theories which have been put forward and which lack the necessary background of exact treatment.

2. *Intraspecific competition for food*

Following the methods used in the case of the other blowflies, newly hatched populations of 500, 1000 and 3000 *C. marginalis* larvae were allowed to develop on 140 g. of fresh, lean beef. Since the weight of a fully grown maggot of this species is 0·1136 g., the 88 g. of consumable meat in the standard ration might be expected to support approximately 775 larvae to maximum-sized maturity. Comparing this figure with the similar assumptions for *Lucilia*, *C. chloropyga* and *C. albiceps*, it is obvious that overcrowding will occur at a lower initial population density of *C. marginalis* than in the other three species.

Taking the ratio of the weight of a fully grown maggot of *C. marginalis* to that of a similar *Lucilia* larvae, the series of pure cultures used in the present tests are equivalent to 953, 1906 and 5718 *Lucilia* larvae respectively. Individual for individual, the *C. marginalis* population commences life in each case with a distinct disadvantage in its relation to the food supply as compared with *Lucilia*. It also compares unfavourably with the other *Chrysomyia* species.

(i) *Mortality*. The mortality observed in the three series of pure cultures of *C. marginalis* larvae is given in table 3, where it is compared with that for populations of the other three species studied. The mortality data are given in round figures, since these are sufficiently accurate for present purposes. The figures for *Lucilia*, *C. chloropyga* and *C. albiceps* are derived by interpolation from the relevant curves (figures 16 to 18).

TABLE 3. MORTALITY IN PURE CULTURES OF *CHRYSOMYIA MARGINALIS* AS COMPARED WITH THAT IN PURE CULTURES OF OTHER BLOWFLY LARVAE HAVING THE SAME INITIAL POPULATION MASS

initial *C. marginalis* larvae	equals *Lucilia* larvae	mortality per cent in populations of			
		C. marginalis	*Lucilia*	*C. chloropyga*	*C. albiceps*
500	953	35	30	32	21
1000	1906	80	40	45	38
3000	5718	89	78	89	76

A general similarity between the *C. marginalis* and *C. chloropyga* data is evident. Biologically, these two species are closely related, differing mainly in size and seasonal occurrence. The higher mortality as compared with *Lucilia* and *C. albiceps* populations of the same density should be noted.

(ii) *Reduction in size*. As with other species of blowflies, and particularly with *C. chloropyga*, a decreasing amount of food per larva is met by the partial compensation of a general reduction in the size of the individuals. This tends to reduce the degree of mortality, but, nevertheless, proceeds side by side with increase in the latter. It is not possible to illustrate this graphically, but the following data for the three series indicate the rate of reduction which takes place in the mean size of the puparium with increasing larval density:

initial larval density	puparial size (mm.)
500	10·19
1000	9·99
3000	7·53

Assuming that a total of 775 full-sized larvae can be produced by the amount of consumable food available, then if all surviving larvae in the 3000 series are full-sized there will be a mortality of 74 % of the population. But in this series there was a reduction in size from the maximum, as shown by the difference in puparial size between this series and the 500 series, of 26 %. There was an increase in the number of small individuals and an increased mortality due to the failure of many of these under-sized larvae to survive.

(iii) *Reduction in fecundity.* A definite relationship between size of individual and the number of eggs which can be produced by each female fly exists in the present instance as shown by the data in table 4. The co-ordinates are plotted in figure 45. Comparison should be made with figure 14.

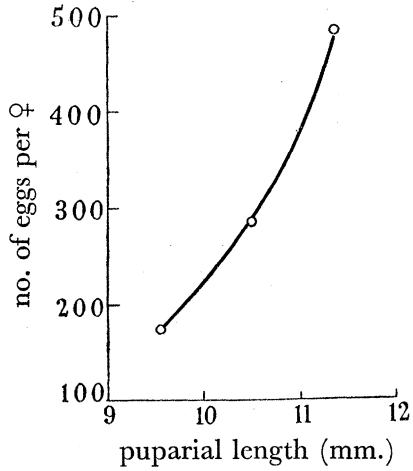


FIGURE 45. *C. marginalis*: relationship between size of female and the number of eggs in the ovaries.

TABLE 4. CORRELATION BETWEEN SIZE OF FLY AND NUMBER OF EGGS IN THE OVARIES: *CHRYSOMYIA MARGINALIS*

mean of size class (mm.)	actual mean size (mm.)	mean number of eggs in ovaries
9·75	9·56	176
10·75	10·51	287
11·75	11·33	486

(iv) *Discussion. C. marginalis* is not a predatory species and does not indulge in cannibalism when confronted with a shortage of food. Because of this, the phenomena associated with intraspecific competition for food exhibit normal features such as are observed in populations of *Lucilia* and *C. chloropyga.* With increasing larval density on a fixed quantity of food, reduction in size of individuals, increase in mortality and decrease in fecundity closely resemble the same events in populations of *C. chloropyga* larvae.

Among the species of carrion-inhabiting flies studied so far, *C. marginalis* is the least well adapted to withstand the adverse conditions engendered by larval overcrowding. Because of its larger size and considerably longer period of growth, combined with the essentially limited nature of available carrion in the field, it is not as well favoured for the production of large populations of adults such as is possible in the case of *Lucilia.* Its general field population might therefore be expected to depend more upon the fluctuations in the number and size of carcasses during any one season than will be found with any of the other flies.

Since the presence of *C. marginalis* has no direct bearing upon the problem of strike in sheep, it is in its relationships to other blowflies which are co-existent with it on carcasses that its true importance lies. In interspecific competition for the common food, its population growth will be still further modified, and it will, in turn, affect that of other species. The extent of this reciprocal interference on the populations concerned will clearly depend upon the inherent limitations of the *C. marginalis* population and upon the nature of the particular species with which it comes into contact. From the data already presented regarding normal larval growth and intraspecific competition, it would appear that *C. marginalis* cannot be expected to show to any great advantage when opposed by any of the preceding three species.

3. *Interspecific competition for food*

(*a*) With *Lucilia sericata*

Two series of mixed populations are available for discussion. These were initially provided with 100 and 500 larvae of each species respectively on the standard meat ration. The mortality and reduction in size of individuals in the case of each species are recorded in table 5.

TABLE 5. MORTALITY AND PUPARIAL SIZE IN MIXED POPULATIONS OF *CHRYSOMYIA MARGINALIS* AND *LUCILIA SERICATA*

		C. marginalis		*L. sericata*		
initial larvae: each species	equals *Lucilia* larvae	mortality (%)	mean size (mm.)	mortality (%)	mean size (mm.)	combined mortality (%)
100	291	38	10·45	14	8·56	29·6
500	1453	63	9·65	17	8·25	46·5

Even with these limited figures, it is clear that *C. marginalis* is at a serious disadvantage when in competition with *Lucilia*. While the latter species is comparatively little affected by the increase in density of the mixed population, *C. marginalis* suffers a severe setback. The mortality in the population of the latter species increases by approximately 66 %, while the length of puparia produced decreases by 7·65 %. In striking contrast, the *Lucilia* mortality is increased by only 22·4 % and its puparial length is decreased by 3·6 %.

It is interesting to compare these figures with those for the very similar situation presented by the admixture of *Lucilia* and *C. chloropyga* under the same conditions. In competition with *Lucilia* and with comparable numbers of initial larvae, *C. chloropyga* suffered a 20 and 42·9 % mortality in the 100 and 500 series respectively; whereas *Lucilia* showed 17·2 and 51·9 % mortalities at the same two densities. The combined mortalities for the mixed populations were 18·8 and 46·7 % respectively. There is therefore a marked difference in the degree of mortality of the individual species in these two different mixed populations, although there is a general resemblance in the outcome of competition.

In the series in which 100 *C. chloropyga* or *C. marginalis* are combined with the same number of *Lucilia* larvae, *C. marginalis* suffers a 90 % higher mortality than does *C. chloropyga*. This may be explained chiefly by the following:

(i) The fully grown *C. marginalis* larva is heavier than a larva of *C. chloropyga* in the same stage of development to the extent of 42·7 %. It presumably requires approximately that amount of extra food to complete its development.

(ii) The total developmental period of *C. marginalis* is 13 hr. longer than that of *C. chloropyga*.

(iii) Larvae of *C. marginalis* reach the beginning of their period of most rapid growth some 10 hr. later than do those of *C. chloropyga*. They are therefore less able to compete with the more rapidly growing *Lucilia* larvae than are the maggots of *C. chloropyga*, since they will be faced with an even greater shortage of food towards the end of their developmental period.

The differences in the mortality of *Lucilia* larvae in the two cases cited may be ascribed to the fact that *C. chloropyga* is markedly superior to *C. marginalis* in its adaptation to the situation. A greater proportion of the food supply is consumed by the *C. chloropyga* population before *Lucilia* has completed its most rapid growth period and therefore less is available to the latter species.

(*b*) With *Chrysomyia chloropyga*

In its reaction to the amount of food available, *C. marginalis* is most closely related to *C. chloropyga.* Its percentage mortality under conditions of intraspecific competition approached that sustained by populations of the latter species, so that in mixed populations it might be expected that something in the nature of straightforward competition for food will take place with results very similar to those obtained in *Lucilia-C. chloropyga* mixed populations. That this is not altogether realized is shown in the data for the available series in the *C. chloropyga-C. marginalis* association. These are given in table 6.

TABLE 6. MORTALITY IN MIXED POPULATIONS OF *CHRYSOMYIA CHLOROPYGA* AND *C. MARGINALIS*

initial larvae: each species	equals *Lucilia* larvae	mortality (%)		
		C. chloropyga	*C. marginalis*	combined
100	325	21	55	41
500	1625	28	97	68
1000	3250	22	98	51

In these series, *C. marginalis* exhibits a comparatively high mortality; while that for *C. chloropyga* is not much more than the normal experimental mortality. There is evidence that the deaths due to experimental conditions or to a natural proportion of fatalities, as the case may be, are higher in *C. marginalis* than in the other species of blowflies. This is also indicated by the fact that, in the present series, *C. marginalis* puparia were of good average size. Allowing for this, however, it is evident that *C. chloropyga* has been much more successful than *C. marginalis,* and this may be ascribed to its more rapid assimilation of food at an earlier stage in the history of the mixed population.

Comparing the series containing 100 larvae of each species with the nearest comparable series giving straightforward competition for food and having a similar initial density in *Lucilia* equivalents, it will be seen that while the *C. chloropyga-C. marginalis* population has a combined total mortality of 40·9 %, the *Lucilia-C. chloropyga* association suffers approximately a 25 % mortality. In this respect it is noteworthy that there is less difference between the growth rates of *C. chloropyga* and *C. marginalis* than between those of *C. chloropyga* and *Lucilia.*

(*c*) With *Chrysomyia albiceps*

Three series are available for comparison, viz. those in which 100, 500 and 1000 larvae of each species were placed initially upon the standard meat ration. The mortality and effect on the length of the puparia in each of the species are given in table 7.

Comparing these data with those for mixed populations of *C. albiceps* and *C. chloropyga* (figure 35), it will be seen that, in the latter case, the combined mortality would have been approximately 26·8, 66·1 and 81·5 % in the respective comparable densities as expressed in *Lucilia* equivalents. The mortality of *C. albiceps* is noticeably higher than in the corresponding *C. albiceps-C. marginalis* populations. The mortality of the *C. chloropyga* population was decidedly lower than that of *C. marginalis* when each of these species was associated respectively with *C. albiceps*.

TABLE 7. MORTALITY AND PUPARIAL LENGTHS IN MIXED POPULATIONS OF *CHRYSOMYIA MARGINALIS* AND *C. ALBICEPS*

		C. marginalis		*C. albiceps*		
initial larvae: each species	equals *Lucilia* larvae	mortality (%)	mean length (mm.)	mortality (%)	mean length (mm.)	combined mortality (%)
100	360	91	10·15	9	10·14	52·50
500	1799	93	8·91	32	9·35	64·25
1000	3597	99	10·31	31	9·16	66·99

The larvae of *C. albiceps* are therefore able to cope with the presence of competing *C. marginalis* larvae much in the same way as they tackle *C. chloropyga* larvae, although they are able to do so in a much more efficient manner and at a much lower initial larval concentration than in the latter case. This is no doubt mainly due to the much slower development of *C. marginalis* and to its greater size, which enables *C. albiceps* maggots to find them more easily and quickly. This also helps to explain the higher mortality of *C. albiceps* (and hence the higher combined mortality) in the *C. albiceps-C. chloropyga* populations, since *C. chloropyga* can survive longer and can consume more food in a shorter time than can an equal number of *C. marginalis* in the *C. albiceps-C. marginalis* populations.

By means of its predatory habits, as well as through the advantages it enjoys by reason of its inherent growth characteristics, *C. albiceps* is therefore able to effect control over a population of *C. marginalis* on a given quantity of medium, provided that the balance of the two species is also favourable.

(*d*) With *Lucilia sericata*, *Chrysomyia albiceps* and *C. chloropyga*

Three series containing 100, 200 and 500 larvae of each of the four species gave the mean mortality data shown in table 8. It is seen that *C. marginalis* is still the least successful species under conditions of interspecific competition when all four blowfly species are present. This is doubtless due to its much slower growth during the early stages of the mixed population. *Lucilia* is also severely affected by the presence of the predatory *C. albiceps*. The position of the three species other than *C. marginalis* is similar to that found in mixed populations of *Lucilia*, *C. albiceps* and *C. chloropyga* described earlier.

TABLE 8. MEAN MORTALITY IN MIXED POPULATIONS OF THE FOUR SPECIES OF BLOWFLIES

	percentage mortality in series containing, of each species		
species	100 larvae	200 larvae	500 larvae
L. sericata	60·5	88·3	99·0
C. albiceps	34·3	37·9	43·6
C. chloropyga	19·5	54·5	47·3
C. marginalis	90·5	92·4	99·4

4. *Discussion*

From the little that has been done with *C. marginalis*, it is clear that this species is not particularly well favoured in the struggle for existence. Where the initial chances of survival would appear to be approximately equal, the more sluggish growth and the necessity for a larger quantity of food per larva render *C. marginalis* comparatively ineffective when in competition with any of the remaining species.

Oviposition by *C. marginalis* on carcasses in the field occurs at a very early stage. According to all records, eggs of this species are found almost as soon as those of *Lucilia*. The laboratory experiments, in which newly hatched larvae of each species were counted on to the meat at the same time, are therefore comparable with what actually happens in nature. They may therefore be used to draw conclusions as to the role played by *C. marginalis* in competition under field conditions.

It is very obvious that *C. marginalis* is at a distinct disadvantage when competing with *Lucilia*, *C. chloropyga* and *C. albiceps*. Very far from being able to exercise control over any one of these species by its inroads upon the food supply or by any other means, it is itself controlled when in mixed populations with them. As a non-predatory fly it could only affect others by some advantage in the rate at which the common food is consumed. It has been shown that, in this, it is inferior even to *C. chloropyga*.

From the experimental evidence, therefore, it would seem that the claim of Mönnig and others that *C. marginalis* is an important controlling factor for populations of *Lucilia* on carcasses was premature and erroneous. Any recommendations based on this contention must be worthless in practice. It will be worth while to study the results of carcass exposures in order to see how the populations of flies fluctuate from time to time and how the various species overlap (and therefore enter into competition) in nature.

VIII. FIELD POPULATIONS OF BLOWFLIES

1. *Sources of material*

The following discussion of field populations of blowflies is based upon published records by various workers and upon data accruing from two years' continuous exposures of carcasses at the Grootfontein College of Agriculture, which is situated in the important sheep-rearing region of the Karroo. The latter data have been supplied to the present writer by Mr A. H. de Vries, Entomologist at the College, who has kindly consented to their use here. A portion of these records was published by Hepburn (1943*b*, p. 71), who, however, did not make any appreciable use of them.

Hepburn (1943*b*, pp. 67 et seq.) also gave data which he had obtained from carcass exposures at Onderstepoort, Transvaal, which has a climate differing very materially from that of the Karroo in that it is bordering upon the subtropical. Unfortunately, these results do not give a continuous record covering even one full year which can be used for depicting the population fluctuations in this locality. The carcasses used varied in size, in the method of exposure and in the number of days during which they were made available for oviposition by blowflies. It is therefore impossible to compare the populations arising from them during any one month with those for other months of the year; nor is it possible to compare these

Transvaal results with those for the Karroo area with any degree of accuracy. Hepburn's results will be used in the following discussion only in so far as they contain marked differences from the Karroo records.

The seasonal fluctuations in the adult fly populations present in the field, as distinct from populations reared from carrion, was studied at Grootfontein by Smit during the two years 1924 to 1926. He used fly traps (Smit 1945) baited with horse-flesh treated with a 1% tobacco extract to prevent development of larvae. The traps were baited and set out in a variety of situations once monthly throughout the period (see Smit 1931, pp. 319 to 333). His results give a very rough monthly index of the numbers of flies of each species which were present in the locality, which visited the traps and were caught by them.

A similar series of trapping results was obtained by Hepburn at Onderstepoort, except that in this case the traps were renewed every week and the catches examined and removed every three or four days. His records extend from May 1940 to July 1942. In the original paper (Hepburn 1943 *a*, p. 18) a graph illustrates the catch per trap per day over the period mentioned.

The data of de Vries are from exposures of one carcass per month throughout the period 1941 to 1943 and give the total of the adult flies which were reared by him from the carcasses. They provide a rough index of the populations actually breeding on carrion during each month of the year, as distinct from the adult fly population which is present. A rough comparison can be made between these records and the data of Smit. Although the records of the two observers were taken during different years (although at the same place), it may be presumed that the general trend of population abundance for each species of fly will not differ so markedly from season to season as to invalidate such a comparison if the whole of the two-year records are used in each case. This presumption is justified by the fact that, in both cases, the periods of abundance coincide during both years for all species.

2. *Inherent deficiencies in the available records*

In several respects, the field records available for the Karroo and other areas lack essential information. To provide data for the basis of a detailed discussion of field populations and their relationship to the available carrion, more intensive field work will be necessary. Some deficiencies in the records at hand will be dealt with briefly at this point.

The records of Smit (1945) were made by exposing one baited trap per month. Carrion remains attractive to any given species of fly for a limited period. After this, the particular species concerned is no longer interested in it as a medium for oviposition and therefore does not visit it. In the case of *Lucilia*, for example, the meat is visited very largely by ovipositing flies during the first day, i.e. while it is still fresh. Later, *Lucilia* is replaced by the Chrysomyias, which again give place to *Sarcophaga* and its allies. There is, as shown by several writers, a definite succession of dipterous visitors which closely follows changes in chemical constitution during decomposition. Hence a trap which is baited with flesh will actually reflect the population of any given species of fly which is present in the area *on only one or, at most, two particular days* during the period over which the trap operates.

The use of one trap per month in an area will therefore give an index of the population of a species on *one* day of that month and will not reflect the actual population density over the whole of the month. Owing to the relatively short developmental period of blowflies generally and to the varied degrees of competition and other vicissitudes to which they are subjected from time to time, fluctuations in the population density of any one species take place fairly rapidly. The one day on which the trap is attractive to a species may happen to be one on which the fluctuations have attained a peak of abundance—or it may happen that at this time the general fly population has just reached a low level. Either of these conditions might be reversed a few days later.

The magnitude of the monthly index as shown by trapping will therefore depend upon the day on which the trap is set up. It becomes a matter, not of the actual density of the fly population during the month but one of chance engendered by the technique. It is clearly necessary to expose baits much more frequently during the month. It is necessary to bear in mind that seasonal changes in weather have an influence upon the length of time during which the bait will remain attractive. During warm weather, the decomposition of carrion takes place more rapidly than during winter, so that the bait remains effective for any given species for a shorter time than in the latter season.

Smit apparently realized this shortcoming, since he states (1945, p. 331) that his trapping records '...give only a general idea of the seasonal distribution'. Hepburn also realized it, since he renewed his traps frequently and mostly used two traps concurrently, one of which contained meat which was 7 days older than the fresh trap (1943, p. 16). His results from trapping adult flies are therefore more reliable as an index of monthly populations than are those of Smit.

Much the same objections rule as regards the exposure of carcasses and the recording of the flies which arise therefrom. A once-monthly test cannot give a true picture of the monthly population which is breeding on the carrion. Furthermore, in order to cover the situation it would be necessary to expose, not only a series of carcasses frequently during the month, but also a number in various sites in a given area at the same time. This presents a practical problem of some difficulty, but, in spite of the amount of labour and number of carcasses involved, such an investigation might be expected to yield results of incalculable value. The annual losses due to blowfly surely justify the expenditure.

In addition to the isolated nature of the carcass records, little information, even of a casual nature, appears to be available as to whether a given species of fly has oviposited or not on those occasions when it was not reared from the carcass. This is an important point if the question of the eliminating effect of competition on the species is to be decided from field data.

Properly planned field observations, carried out in an area in which the blowfly is a major problem, are necessary in order to determine the exact interrelationships of the various species in nature. The available records will be examined here in order to compare the information with the laboratory findings. It is evident, from what has been said, that this must be regarded purely as a preliminary discussion.

3. *The seasonal abundance of adult flies*

(*a*) *In the Karroo*

A brief recapitulation of Smit's results with baited fly traps will be given here. Smit noted that the different species of flies varied in numbers very considerably at different times of the year and that each species had a definite period during which it became most abundant.

The records for the two seasons were very similar, the periods of abundance and scarcity practically coinciding for each species. There were two periods during which blowflies in general were caught in large numbers in the traps, namely, during the summer and autumn. All flies became very scarce in winter. Briefly stated, the relative abundance of the four main species was as follows:

(i) *C. chloropyga*. This was the most generally abundant species. It became very numerous during October to December and, to a smaller extent, during March to May. It occurred in the traps throughout the year.

(ii) *L. sericata*.* This followed *C. chloropyga* in order of abundance during the early summer (October to December). Another peak occurred in April and May, but it was then less numerous. On the whole, it was not as well represented in the traps as either *C. chloropyga* or *C. albiceps*. Flies were caught throughout the year.

(iii) *C. albiceps*. This species was abundant during the summer (November to January) but not to the same extent as the two preceding species. Maximum catches occurred during April and May, when it was the most numerous of all the flies. It was present in the traps throughout the year, although in very small numbers from June to October.

(iv) *C. marginalis*. The period of maximum abundance was from March to May. It occurred during the autumn but from June to September it disappeared entirely, reappearing in the early part of summer.

Broadly speaking, it can be said that, of the four species, *C. albiceps* and *C. marginalis* were essentially summer species, whereas *Lucilia* and *C. chloropyga* were more prevalent during spring or early summer. This conclusion is true only if the traps were equally effective throughout the year in attracting the adult population of blowflies present in the area. As will be seen later, there is reason to believe that this was not the case with all the species.

(*b*) *In the Transvaal* (*Onderstepoort*)

The records obtained by Hepburn at Onderstepoort are given by him in the form of a graph showing monthly averages for the catch per trap per day (see Hepburn 1943 *a*, p. 18). They differ considerably from those of Smit above. At Onderstepoort, all of the four species of blowflies were found in the traps throughout the year and appeared to be more abundant at all times than at Grootfontein. Furthermore, the peaks of abundance of the four species all more or less coincided.

Lucilia, *C. albiceps* and *C. marginalis* were taken in greatest numbers during the summer months (November to January) and continued to be comparatively plentiful during autumn and early winter. On the other hand, *C. chloropyga* catches reached their peak in the spring (September to October) and diminished during the summer. It is noteworthy that *C. marginalis* was the least abundant of the four species throughout, the numbers caught per day being always very small.

This difference in seasonal distribution as reflected in the traps at the two centres is no doubt due to climatic differences. In the Onderstepoort district, as in many parts of the Transvaal, the difference between summer and winter temperatures is not as great as in the Karroo. Furthermore, the atmospheric humidity never falls as low in the Transvaal

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* These records include flies of *L. cuprina* which was not then recognized as a separate species. This makes no difference in the present discussion, since the species of *Lucilia* are treated here together.

during winter as it does in the Karroo. In the former region, all species are able to breed throughout the year given suitable carrion. Although winter breeding is necessarily somewhat restricted as compared with summer breeding, there is nevertheless a sufficiently large population of emerging flies to account for the rapid increase in all species during spring and summer.

The effect of weather on the carcass is important. In the Karroo areas, the winter is severe and the decomposition of carrion is markedly retarded. It therefore remains suitable for the development of *Lucilia* and *C. chloropyga* for relatively long periods, and these species are able to breed in larger numbers than when summer heat or the warmer winters of the Transvaal hasten decomposition and thus restrict the period during which the carcass remains attractive.

(*c*) *In the winter-rainfall area*

Mönnig & Cilliers (1944) have described the results of trapping adult flies during the course of a year in the Bredasdorp district of the south-western Cape Province. Here the temperature is normally moderate and the relative humidity is high with no marked daily or seasonal fluctuations. It never becomes very cold in winter nor very hot in summer.

The numbers of flies found in the traps for each month are given by them in a table which shows each species separately. When these figures are treated, as were those of Smit (see above), they give a proportional distribution of the adult fly population of each species over the 12 months substantially the same as that obtained with the Grootfontein records. Grootfontein is situated in the summer-rainfall area, and the winters are cold and very dry. This difference in climate makes no difference to the seasonal abundance of blowflies, although it does influence the incidence of strike in the living animal.

(*d*) *Sources of fly populations*

The trapping results show that the populations of adult flies in the field exhibit fluctuations in density which are clearly related to seasonal influences. Since the peaks of abundance evidently result from the accumulation of emergents from pre-existing larval breeding grounds, these seasonal changes must produce their effect during the development of larvae and must determine the extent of oviposition by the parent flies upon the food medium. Furthermore, since the life of adult flies is comparatively long, it is easy to see how large populations can arise through accumulation over a period of time.

Similarly, scarcity of flies in the traps must either result from the ineffectiveness of the traps at certain periods or from an actual scarcity of flies in the area. The latter contingency would arise if breeding were restricted or entirely stopped at certain times of the year. The effect of seasonal breeding tends to produce violent seasonal fluctuations in the populations of adult insects concerned, and this is what appears to happen in blowfly populations.

Mönnig & Cilliers (1944) have maintained that the fly known as *L. cuprina* breeds almost exclusively on live sheep throughout the year. This contention cannot be seriously sustained in view of the very large population of the form *L. cuprina* which is undoubtedly present in the field at certain times and of the actual records of breeding upon carcasses in the tests about to be discussed. There is no doubt that carcasses, of various types, constitute the main source of all the species of blowflies. It is to these that we must look for the source of the adult fly populations recorded in the traps.

4. *Seasonal abundance of species on carrion*

(*a*) *Carcass exposures at Grootfontein*

The observations made by de Vries at Grootfontein were based upon the exposure of two series of carcasses. In one of these the fresh carcass was exposed to the visitation of blowflies for 3 days; in the other, the carcass was allowed to lie out for 10 days. One carcass in each series was used per month and the series ran continuously from July 1941 to April 1943. Flies breeding from each carcass were collected, sorted and recorded.

Since there is practically no difference in the relative abundance or occurrence of the four species between the two series, the 10-day exposures will be used for discussion. The data supplied by de Vries are plotted in figure 46.

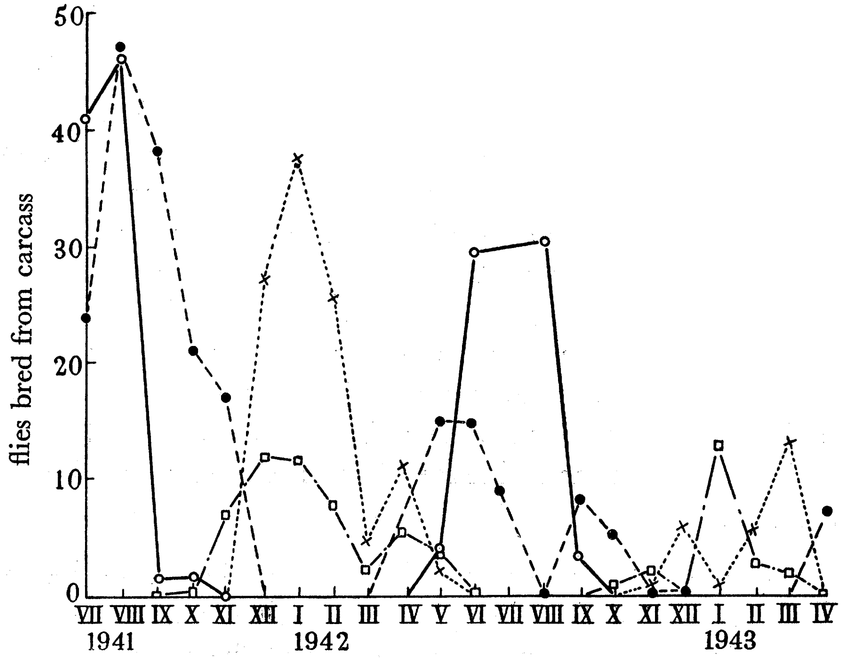

FIGURE 46. Carcass exposures at Grootfontein College of Agriculture, Middelburg, Cape Province, during 1941 to 1943. Carcasses exposed for 10 days once each month. Graph plotted from data supplied by A. H. de Vries. o, *L. sericata*; ●, *C. chloropyga*; □, *C. albiceps*; ×, *C. marginalis*.

There is a distinct seasonal trend with all species. *Lucilia* (including *L. sericata* and *L. cuprina*) is characterized by heavy breeding on carrion during the winter months (May to September) and its complete absence in the emergent population of flies during summer. The same is virtually true of *C. chloropyga*, although this species was present throughout the year but in very small numbers during the summer. On the other hand, *C. albiceps* and *C. marginalis* populations reach their peaks concurrently during the summer, the former being also present in small numbers during winter while *C. marginalis* disappears from the carcass during the cooler months.

The beginning and end of the breeding season for each species overlap those of other species. The extent to which this occurs has already been discussed when dealing with interspecific competition. Apart from this, it can be said that the bulk of the larval populations on carrion are sharply divided into summer breeders and winter breeders. The greatest degree of interspecific competition for the available carrion will therefore take place between the species belonging to the same seasonal group. In other words, this phenomenon will be most marked between *Lucilia* and *C. chloropyga* or between *C. albiceps* and *C. marginalis*. The possibility of competition between members of opposite groups will obviously depend upon the extent to which their populations overlap, and this is strictly limited.

(*b*) *Carcass exposures at Onderstepoort*

Hepburn's results at Onderstepoort are given in his paper (1943*b*, p. 67) in the form of a table. For reasons already given, the data cannot be presented in graphic form as in the case of the Grootfontein figures. A general idea of the position can be given briefly here.

The records of flies breeding from carcasses are similar to those from Grootfontein, although the seasonal breeding of the various species is extended on account of the warmer winter months in the Transvaal centre. Again, *Lucilia* and *C. chloropyga* are present mainly during the cooler months, while *C. albiceps* and *C. marginalis* breed mostly during the summer. The range of the two latter species, however, is here extended into April and commences in August. The records are variable and are not sufficiently complete to give a clear picture of the situation.

5. *Relationship between fly and larval populations*

Since the Onderstepoort records are unsatisfactory, attention will be confined to the Grootfontein data of Smit and de Vries. Since these are taken in a sheep-raising area, they will be more applicable to the problem in hand than are those obtained in a district which is not.

The two sets of data having been taken in widely different ways and having to do with widely different populations, it is not possible to compare them directly with one another. The figures of Smit and de Vries have therefore been treated as follows. In Smit's paper, the records are given in separate tables for each species. Monthly totals for each trap are given, and the grand total for all the traps is shown at the foot of the monthly column. This monthly total for all traps was expressed as a percentage of the yearly total for all traps. By this means, the proportion of the yearly fly population present in any one month was obtained.

A similar procedure in the case of the carcass populations was followed, giving the proportion of the yearly carcass population of any species present in any given month. In both cases, the percentage figures were calculated on the average of the two years' records.

The two sets of figures are plotted in figure 47. Each species has been treated separately for the sake of clarity. This method brings out clearly the essentially seasonal character of blowfly incidence and helps to explain the relationship between blowfly breeding and adult fly abundance during the year.

In a general way, it can be said that the build-up of the adult population of each of the four species is closely dependent upon the extent to which larval breeding and competition occurs on carcasses. A very marked difference, however, is shown between the species constituting the two seasonal groups referred to above. In the case of *Lucilia* and *C. chloropyga*, which breed most extensively during the winter months, the adult population assumes its peak of abundance during summer. According to the trapping records, therefore, a very small proportion of the total yearly population of adult flies is present in the field during the period when there is undoubtedly a high population arising from larval populations on carrion. Conversely, there would appear to be little or no breeding on carrion at the time when the adult fly population is recorded as being at its peak. This phenomenon is more marked in the case of *Lucilia* than in that of *C. chloropyga*, since the latter fly is still emerging, although in reduced numbers, during the early part of summer.

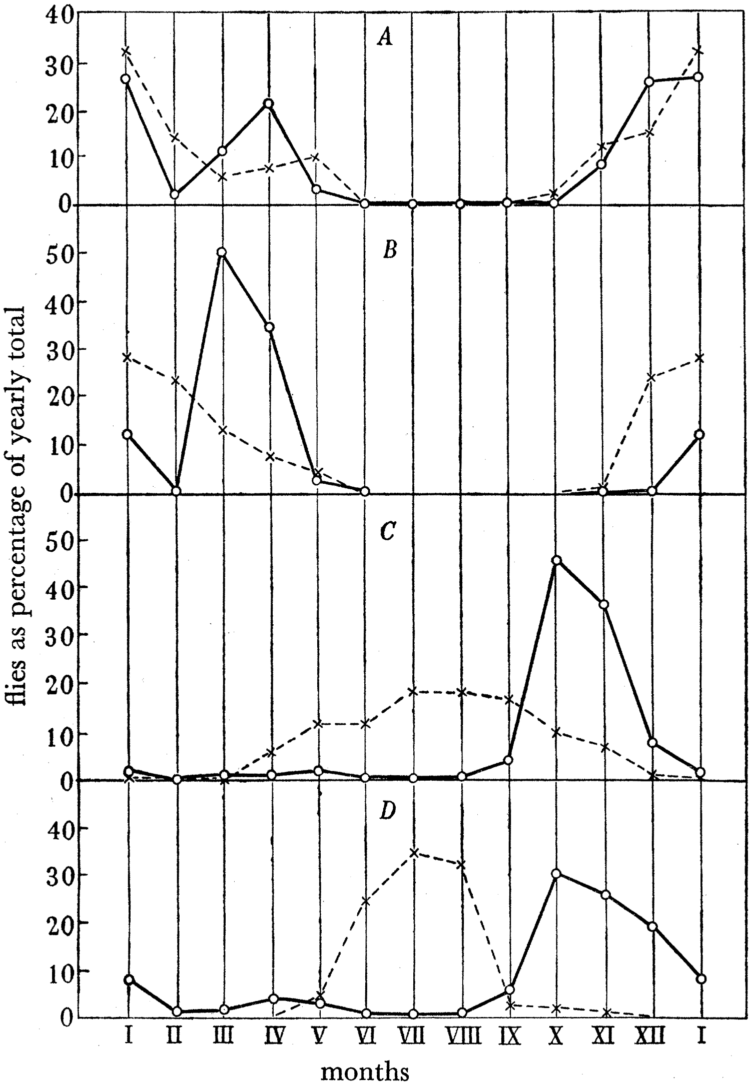

FIGURE 47. Seasonal distribution of fly populations at Grootfontein as shown by fly-traps during the period 1924 to 1926 (data from Smit 1931) and carcass exposures during 1941 to 1943 (de Vries's data). Populations are expressed as percentages of yearly totals. *A*, *Chrysomyia albiceps; B*, *C. marginalis; C*, *C. chloropyga; D*, *Lucilia* spp. o Traps. × Carcasses.

In the case of the summer breeders on carrion there is a totally different relationship. Here, the graph for carcass emergents and the total fly population recorded by traps very roughly coincide, the agreement being more pronounced in the case of *C. albiceps* than with *C. marginalis*. Thus, when breeding on carrion is taking place, the fly population as recorded by traps gradually increases largely, it would appear, as a result of a gradual accumulation of the emergents from carcass populations. This contrasts sharply with the sudden increase in fly populations evinced by *Lucilia* and *C. chloropyga*. Furthermore, when carcass breeding by *C. albiceps* and *C. marginalis* ceases during winter, few or no flies are recorded in the traps —again in marked contrast with *Lucilia* and *C. chloropyga*.

Validity of trapping records. In view of the rather remarkable outcome of the comparison in the case of the two primary flies, it seems pertinent to question the validity of the trapping method as a means of obtaining an index of the fly populations of these two species. Records obtained from carcasses can be accepted as approximately correct since it is known what species are, or are not, present on the carcass at any given time. It is also reasonable to assume that, when no breeding occurs on carrion at any particular time, either the carcass is not in a state which is attractive to the species of fly concerned or there are few or no flies present in the area at that time. That no flies are recorded in traps during the period when no breeding occurs on carrion is therefore understandable.

When breeding is occurring on carrion, however, a parent population of flies must be present to produce the larval population. Furthermore, it follows that the density of the parent population must be roughly proportional to the density of the population of progeny to which it gives rise. An increase in the fly populations of *Lucilia* and *C. chloropyga* might reasonably be expected during the winter, following the reasoning here; but no such increase is recorded by the traps. The records obtained from these traps must therefore be suspect at this season of the year in the case of these two species, although they appear to give reasonably good results with *C. albiceps* and *C. marginalis*.

This failure of traps is probably closely related to the question of the amount of available carrion in a state which is suitable for oviposition by *Lucilia* and *C. chloropyga* adults. It is also probably true to say that more carrion is available in the field during the more rigorous winter season than during summer, and that there is a greater degree of attraction to such feeding and breeding grounds. In consequence, few flies are attracted to the comparatively insignificant quantity of bait in the traps.

It is during the summer, when the greater proportion of the fly population appears to be so little occupied in finding carrion that it will visit traps, that the greatest incidence of strike in living sheep occurs. In this connexion it will be recognized that the conditions inducing strike change only slowly on the living animal, so that the period over which a given animal will constitute a source of attraction to primary flies will be much longer than that of a carcass. Individual sheep, however, do not offer the degree of attraction afforded by a single carcass, and this remains true even of a group of attractive animals. Traps placed in the area will therefore not be ignored to the same extent as when suitable and sufficient carcasses are available.

For a more detailed account of the use of traps as a means of gauging fly populations, reference should be made to the paper by Davidson (1933).

6. *Summary of main facts*

In spite of the drawbacks associated with the methods employed in recording field populations of blowflies, certain information has been obtained and is summarized here, since it will be used in the discussion which follows.

(1) The four species exhibit definite seasonal trends, both in their breeding period on carrion and in the incidence of their adult fly populations in the field.

(2) They may be divided into two seasonal groups, viz. (*a*) Summer breeders: *C. albiceps* and *C. marginalis*. (*b*) Winter breeders: *Lucilia* spp. and *C. chloropyga*.

(3) In traps, the maximum abundance of *C. albiceps* and *C. marginalis* occurs during the summer and coincides with the breeding on carrion. The corresponding periods in the case of *Lucilia* and *C. chloropyga* occur during summer and therefore do not coincide with maximum larval breeding.

(4) During winter, *C. albiceps* does not occur on carrion and the fly population is extremely small. Populations of *C. marginalis* are non-existent at this time.

(5) A certain amount of overlapping occurs between the populations of summer and winter groups, but at these times the populations of both are usually small.

The above is true of blowfly populations in the Karroo. In general, much the same situation exists in the Transvaal. There is, however, a certain degree of modification due to climatic influences and overlapping of summer and winter populations is usually marked.

IX. Field populations and competition for food

The laboratory data can now be reviewed in the light of the field records. From the nature of the latter, the information which it is possible to obtain from any comparison will be fragmentary. In view of the deficiencies in the field data, in particular regarding the actual degree of oviposition by the various species on carcasses, no clear-cut agreement between laboratory and field results can be expected. This must await more intensive field work. Nevertheless, some impressions may be formed and some limited conclusions drawn regarding the interrelationships of the various species and the effect of competition for food in the limitation of the general fly population.

From figures 46 and 47, it is clear that a single species rarely, if ever, inhabits a carcass to the exclusion of all others. Intraspecific competition, *per se*, is the exception in nature. The most intense competition will normally occur between the two species belonging to the same seasonal group. During the limited periods of overlap between the populations of different groups, all four species may compete for the available carrion; but, at these times, the populations of all are comparatively small, and competition will be correspondingly less intense.

The phenomena may be studied conveniently under three main heads, viz.:

(1) Competition between the primary flies (winter group).

(2) Competition between the secondary flies (summer group).

(3) Competition between primary and secondary species (overlap periods).

1. *Competition between the primary species*

Lucilia and *C. chloropyga* belong to the same seasonal group. The populations of both species follow a very similar course, except that, in the case of *C. chloropyga*, small populations are present throughout the year, and that the graph for relative abundance (figure 47) does not rise and fall as steeply as with *Lucilia*, neither does it attain to a definite high peak as in the latter species. This is shown also in figure 48 *A*, where the actual numbers of flies bred from carcasses are shown as related to season.

Attention is drawn, in the first instance, to the form of the graph for *Lucilia* populations in figure 47. The typical logistic curve for population growth is followed by the relatively steeply descending curve as the number of individuals inhabiting the carcass progressively increases beyond the maximum possible population which can be supported by the given amount of food. The growth and decline of *Lucilia* populations arising from carcasses in the field clearly follows the general course observed in the laboratory for intraspecific competition. There is nothing in its character, when taken alone, to suggest interference by another species.

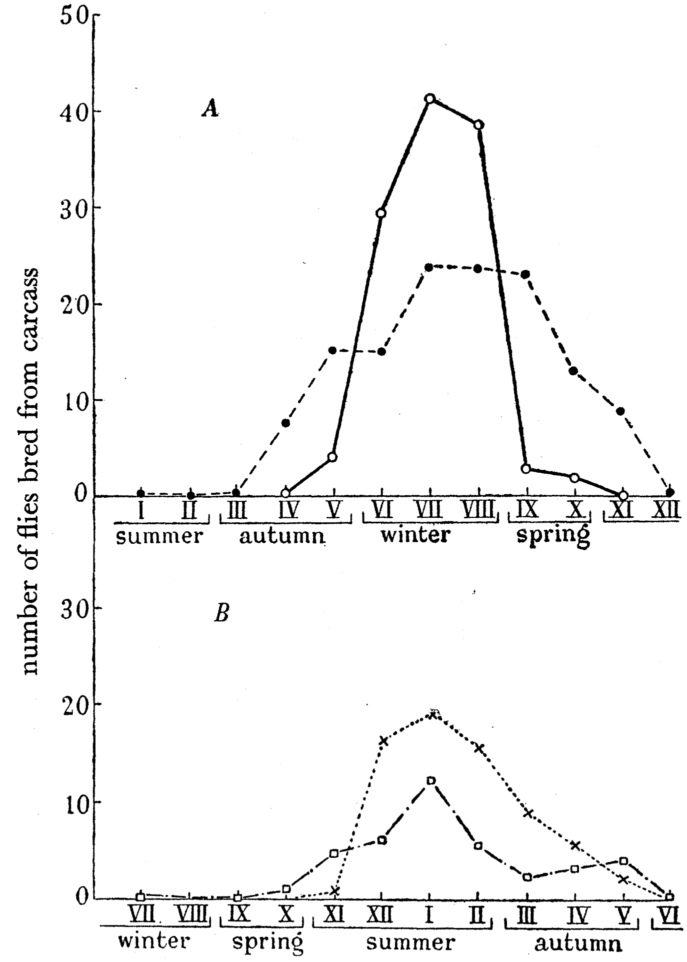

Figure 48. Number of flies reared from carcasses at Grootfontein (average of 2 years). *A*, primary group; *B*, secondary group; ○, *L. sericata*; ●, *C. chloropyga*; □, *C. albiceps*; ×, *C. marginalis.*

It is known, however, that *Lucilia* was at this time co-existent with a population of *C. chloropyga*, with which it was competing for a common food supply throughout the breeding season. In the laboratory experiments, the gross result of interspecific competition, when expressed in terms of population mass, did not differ materially from that achieved by simple intraspecific competition. In the case of *Lucilia*, the general course was also observed when this species was living in pure cultures and the addition of the *C. chloropyga* larvae had merely the effect of intensifying the intraspecific struggle. This is corroborated by the field records.

Laboratory populations of *C. chloropyga* larvae were less successful in surviving the interspecific struggle than were *Lucilia* larvae. This is evident in the field populations. Instead of increasing and decreasing in the manner which is familiar in pure cultures, the graph for *C. chloropyga* flattens out very markedly during the period when a high, sharply defined peak of abundance would be expected and the following decrease in population is gradual instead of rapid. It is obvious that, had such a peak been exhibited, it would have occurred at approximately the same time as that of *Lucilia.*

If due allowance be made for the presence of other environmental factors such as parasitism, weather conditions and the like, which will tend to alter the balance between the two species in the field, the association of *Lucilia* and *C. chloropyga* on carcasses clearly produces results which are very like those arising in laboratory cultures. The superiority of *Lucilia* in interspecific competition with *C. chloropyga* on carcasses is indicated by its attainment of a normal type of population growth. It is also able to produce a much larger maximum population of flies than the latter species (figure 48 *A*). Association with *Lucilia* serves to reduce the maximum of the *C. chloropyga* population, the curve for the latter species being flattened out over the peak period.

If the carcass used in the field exposures is regarded as a sample of all carcasses present in the area at a given time, then competition between these two primary species cannot be said to produce any useful measure of control over either. While the presence of *Lucilia* serves to reduce the numbers of *C. chloropyga* which survive, its population must also be reduced by the competition of *C. chloropyga* maggots. This was demonstrated in the laboratory, and there is no reason to doubt that it happens in nature. The extent of the limitations thus imposed will vary with a number of factors, some of which will be enumerated later. There is no evidence that *Lucilia* can eliminate *C. chloropyga* from the carcass, although it is the superior species. Neither can *C. chloropyga* reduce the available food supply to the extent where *Lucilia* suffers severely from starvation.

Fluctuations in fly populations take place from year to year as a result of changing environmental factors. In certain seasons there will be much higher populations of one or another species than usual. This will be followed by an intensified competition on the carcass, with the balance of the species altered. The two seasons covered by the records at Grootfontein indicate a slight alteration in the balance between *Lucilia* and *C. chloropyga* (figure 46), this being in favour of the former species during the second season.

2. *Competition between the secondary species*

For the present purpose, *C. marginalis* is regarded as a secondary fly although it does not attack the living sheep. The *C. albiceps* population commences to breed actively in the spring (October), reaches a peak during January and then declines more or less gradually until it becomes almost non-existent by June. The *C. marginalis* population, while following a somewhat similar course, commences slightly later than *C. albiceps.* Breeding begins in November, rapidly increases to a maximum during December to February, and then falls to zero by the beginning of June. The decline in the population is also a gradual one.

The effects of interspecific competition between the two species, as shown by carcass records, are not as well defined as in the case of the primary flies. From the form of the graphs for the two populations, a general resemblance to the *Lucilia-C. chloropyga* association may be seen. In the case of the secondary flies, *C. albiceps* takes the place assumed by *Lucilia* in the primary association. The same rapid rise to a well-defined peak takes place (figure 48 *B*). With *C. albiceps,* however, the decline which follows is not abrupt. This is probably to be ascribed to its predatory and cannibalistic habits which give it an added survival value.

The place of *C. chloropyga* is here taken by *C. marginalis*, and an indication of the typical flattened or rounded curve obtained with the former species is seen with the latter. Although the total population of *C. marginalis* is larger than that of *C. albiceps* at the peak period, there is some evidence of a limitation imposed by the latter species, especially at the time of maximum breeding, but this is not very definite. Taking the *C. marginalis* population by itself, it could be argued that the form of the curve is not significantly different from one depicting the normal growth and decline of a population developing on a limited but constant food supply. Consequently, it is not possible to draw any definite conclusions from the present records as they stand.

Since the laboratory evidence has shown that *C. albiceps* is inimical to *C. marginalis* in mixed populations, it is probable that the initial field population of *C. albiceps* is always small in comparison with that of its competitor. To account for this, it is necessary to postulate some factor, other than competition, which acts to limit the *C. albiceps* population in a manner severe enough to prevent large numbers of parent flies from emerging and depositing eggs on the carcass. Such a factor does exist, and *C. albiceps*, more than any of the other species, is particularly susceptible to its influence.

This limiting factor is pupal parasitism by the Pteromalid, *Mormoniella vitripennis* Walk., which is present in the vicinity of carcasses in summer. This will be dealt with elsewhere, but it may be mentioned here that owing to the pupation habits of *C. albiceps* a large proportion of puparia are normally accessible to the parasite. The value of *C. albiceps* as a limiting factor in blowfly populations through interspecific competition and predatorism is therefore considerably reduced.

3. *Competition between primary and secondary species*

To illustrate the extent of overlapping between the two groups of flies, the average monthly records from carcass exposures for the two years are plotted in figure 49.

Overlapping of larval populations on carrion occurred as follows, taking the species in pairs:

(*a*) *Lucilia* and *C. albiceps* were co-existent during May, June, July, September, October and November. During these months, the *C. albiceps* population was comparatively small. From May to July it was decreasing while, during the period from September to November it was increasing gradually. The latter period coincided with the end of the *Lucilia* breeding on carrion. The population of *Lucilia* had, by then, decreased very rapidly in what may be regarded as a normal manner at a time when no *C. albiceps* population was present. There is therefore no reason to believe that *C. albiceps* has anything to do with the decline of *Lucilia* populations on carrion. This decline must have resulted mainly from intra- and interspecific competition within the primary group.

(*b*) *Lucilia* and *C. marginalis* exhibited the same general relationship. In this case, *C. marginalis* was absent from the carcass during the whole of the period from June to October, i.e. during practically the whole of the main breeding period of *Lucilia*. It can be concluded that *C. marginalis* did not influence the growth and decline of the *Lucilia* population.

(*c*) *C. chloropyga* and *C. albiceps* overlapped throughout the year except during August, when *C. albiceps* was absent. During the period from February to July, *C. chloropyga* was increasing while *C. albiceps* was declining; from September to January the reverse was the case. On the strength of the recorded populations at these times, *C. albiceps* cannot be held responsible for initiating the decrease in the *C. chloropyga* population in spring. The *C. albiceps* population was not sufficiently numerous in the autumn to affect materially the increase of *C. chloropyga*. The winter breeding of the latter species was therefore very little, if at all, influenced by the presence of *C. albiceps*.

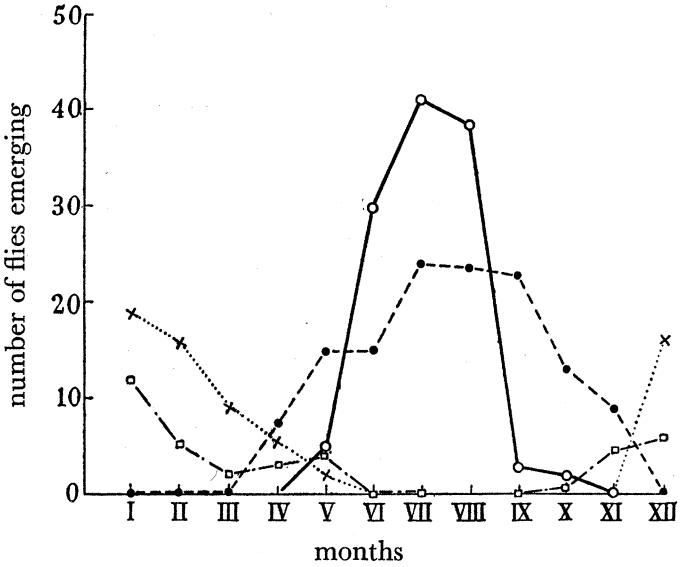

FIGURE 49. Overlap between populations of the different species of flies on carcasses. ○, *L. sericata*; ●, *C. chloropyga*; □, *C. albiceps*; ×, *C. marginalis*.

(*d*) *C. chloropyga* and *C. marginalis* presented a similar picture. It is obvious that *C. marginalis* did not cause the spring fall in the *C. chloropyga* abundance, nor was it able to prevent the increase of the latter in the autumn, although at this time its population was higher than that of *C. albiceps* and was approximately equivalent to that of *C. chloropyga*.

When the species are taken pair by pair, there is no evidence for postulating any material degree of control by one group over the other. At certain times, however, more than two species lived together on the carcass as indicated by the emergence of flies. This occurred as follows:

(i) Threefold competition must have taken place between the following species:

Lucilia, *C. chloropyga* and *C. albiceps* during June, July, September and October. The population mass of *C. albiceps* was small throughout and varied from approximately 0·06 % of the total population mass in July to a little over 6 % in October.

C. chloropyga, *C. albiceps* and *C. marginalis* during January, February, March, April and December. The population of *C. chloropyga* was very small at these times with the exception of April, when it exceeded that of either of the other species and when the population mass of this species was approximately 39 % of the total mass of all species.

(ii) A fourfold competition took place during May and November. During May, the two secondary species were responsible for approximately 30 % of the total population mass;

while during November, this figure increased to 41%. At these times, therefore, when competition might be expected to be in its most severe phase, the primary species were in the ascendancy.

From the above review of the available records, it might be concluded that:

(1) *Lucilia* populations are relatively unaffected by the flies belonging to the secondary group.

(2) Populations of *C. chloropyga* are more exposed to competition with secondary species, since they are present during summer when the weight of the combined *C. albiceps*-*C. marginalis* populations may serve to check their increase at this time. During winter, however, they are faced with competition with *Lucilia* alone.

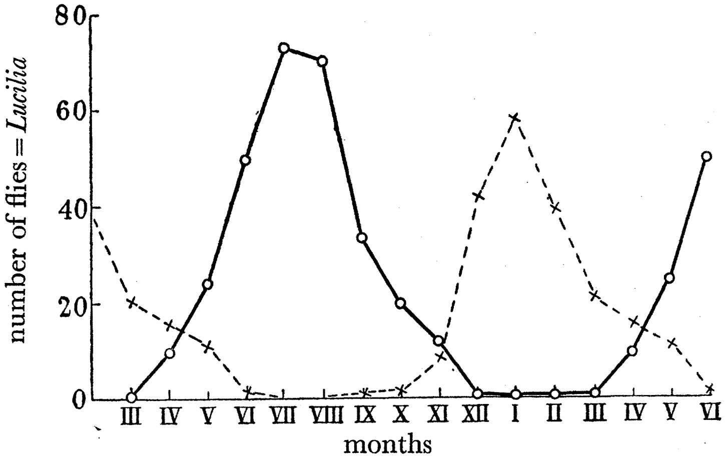

FIGURE 50. Overlap between populations of primary and secondary groups of flies on carcasses. The numbers of the flies are expressed as '*Lucilia* equivalents'. ○, primary species; ×, secondary species.

Before accepting these conclusions, it is desirable to have information as to the initial populations present throughout the year on carrion. From emergence records alone, it is not justifiable to say that, because a species is absent it is therefore controlled by other species which happen to be present. The fallacy of such an argument immediately becomes apparent from an example. *Lucilia* breeds on carcasses during the winter but disappears during summer; *C. marginalis* is obtained during the summer, but not during winter. Comparing the graphs of these two species, one could conclude either that *Lucilia* controls *C. marginalis* or that the reverse is true. Neither conclusion is correct.

This point is brought out clearly by grouping the populations of the summer breeders and the winter breeders and plotting the two groups separately on the same chart (figure 50). The graphs have been continued over more than 12 months in order to include the complete records of both groups side by side.

The combined mass of the populations of secondary species commences to increase only *after* that of the primary flies has become depleted and is on the point of virtual disappearance. Similarly, the primary population begins to build up at a time when the secondary population has virtually died out. The picture thus presented is incompatible with any theory which postulates a controlling influence by one group over the other. It suggests, on the contrary, that breeding activities on carcasses are mainly seasonal in character.

If this is accepted, then competition for food between the species can only affect those occurring in the same seasonal group. Consequently, it is easy to see why competition alone can never reduce *Lucilia* populations to the point at which they cease to present a major practical problem.

X. Some factors influencing competition

Straightforward intra- or interspecific competition for food will be rare in nature. A number of different factors may combine to affect the course of competition and hence to influence the results arising therefrom during the season. The operation of any or all of these factors may tend to mask the outcome of competition itself. One such agent, namely parasitism, has been cited in the case of *C. albiceps*. Some of the main factors which influence competition either directly or indirectly are enumerated below and their effects discussed briefly in order to indicate the desiderata for future work.

1. *Availability of carrion*

(*a*) *Quantity and sources*

Competition is basically governed by the quantity of consumable food available per larva in any given population. Its effectiveness in limiting the fly population within a given area will depend upon the number and sizes of carcasses (i.e. upon the total mass of consumable carrion) per unit area at any given time. No definite figures are available as to the approximate number of dead bodies of animals to be found at various times of the year, but this no doubt fluctuates very widely, with seasonal and other factors, both from time to time and from place to place. No quantitative survey can therefore be made at this time, and it must suffice to examine the sources and causes of fluctuations in the supply of carrion.

The supply of cadavers does not rest solely with the populations of sheep or other large domestic animals within a given area. It is doubtful, indeed, whether these provide more than a small proportion of the blowfly breeding grounds, although the extensive rearing of sheep over large tracts of country tends to the production of an increasing number of carcasses which remain undiscovered until after they have given rise to a population of flies. It is more probable that the main source of blowfly populations is to be found in the dead bodies of the innumerable smaller wild animals which abound in the field and which are rarely seen by the casual observer. These animals exhibit a wide range in size and habits and include such diverse forms as birds, reptiles and mammals.

In his paper, Hepburn (1943 *b*, p. 72) gives some records of blowflies bred from a variety of small carcasses exposed at various times of the year. These records provide convincing proof of the importance of these animals in maintaining large populations of flies of all species in nature. To quote from Hepburn's table, the following emerged from the carcass of a cat: 1367 *L. sericata*, 6410 *C. chloropyga* and 156 *C. albiceps*. A rat carcass gave rise to 571 flies of *L. sericata* and 50 of *L. cuprina*; while a dead snake was responsible for 341 *C. chloropyga*, 1458 *C. albiceps* and 161 *C. marginalis*. Birds were represented by a dead fowl which produced 188 *L. cuprina*, 26 *L. sericata*, 11 *C. chloropyga* and 2986 *C. marginalis*.

Some of these small carcasses showed a great variation in the species of flies produced. This happened even when two of the same species of animal were exposed simultaneously close together. Fuller (1934) records a similar variation in Australia, and notes that certain kinds of maggots are more numerous on certain dead animals. Thus, a cat always has more *Chrysomyia* larvae breeding on it than does a guinea-pig, the latter having a preponderance of *Lucilia* and *Calliphora* maggots. Hepburn's results do not altogether agree with this suggestion of choice of carcasses by flies, and he considers that the matter is purely one of chance. On the other hand, Mönnig & Cilliers (1944) conclude from their observations in the winter rainfall area of the South-west Cape Province that *Lucilia* breeds mainly on small carcasses and seems to prefer them to large ones.

The question requires more extensive investigation, particularly as it has a bearing upon the intensity of competition which takes place on what is probably the most prolific source of blowfly populations. If specific preference for certain kinds of carcasses does exist, then interspecific competition on the whole will be very much less intense than is generally assumed to be the case, although intraspecific competition will tend to be more severe.

One of the most important of the many small animals which form the source of carcasses in South Africa is the 'dassie' or rock-rabbit. A number of species or subspecies of this familiar mammal occur in Africa, those in the southern portion being forms or subspecies of *Procavia capensis*. In the Karroo area, dassies have become so abundant during recent years that they constitute a major problem in themselves. Normally living among the rocky hills and kopjies of the region, they have multiplied to such an extent that the food supply in these habitats has become insufficient for their needs, and they have been driven to search for means of subsistence among the crops and pastures of the lower-lying farms. Other small animals, such as rats, mice, birds and reptiles, also abound in the area and contribute their quota to the annual supply of carrion.

In order to gain an idea of the quantity of carrion which thus becomes available during the course of the year, it would be necessary to make general population surveys of the wild fauna at regular intervals over a given area and to ascertain the extent and causes of mortality in the case of each species. In the absence of such information it may be assumed, from *a priori* considerations, that the increasing population of an animal like the dassie must entail a progressively increasing proportion of deaths to births, and that the number of carcasses which become available day by day is, at the present time, steadily and rapidly rising. If the blowfly population is taken as an index of the quantity of carrion which is available for breeding, then this assumption is substantially correct.

(*b*) *Fluctuations in quantity*

The quantity of carrion in a given area will not remain constant, or even approximately so, from month to month or from year to year. Considerable fluctuations must occur. These are governed by two main, interrelated factors, viz. (1) the population densities of the animals concerned and (2) the mortality factors which operate within those populations. Thus the production of carcasses is almost entirely independent of events which may occur in the populations of blowflies which use them as food. According to Nicholson (1933), food consists of objects which are produced in quantities that are entirely independent of the activities of the animals searching for them. On occasion, however, the blowflies themselves are responsible for mortality among animals, either directly or indirectly.

Severe incidence of strike in sheep may result in the death of the animal if neglected; or flies may indirectly cause the death of an animal by the part they play in the transmission of pathogenic organisms. Theiler *et al.* (1927) found that the three species of *Chrysomyia* are important agents in the transference of the anaerobic saprophyte, *Clostridium parabotulinum bovis*, from one carcass to another. The toxin produced in carrion by this organism is the cause of 'lamsiekte' (parabotulism) in cattle which, through suffering from osteophagia, are induced to eat the debris of carcasses in an attempt to remedy the deficiency of phosphorus in the vegetation. Deaths in which the flies themselves take part directly are probably a comparatively insignificant proportion of the total and are probably more widely true regarding domestic animals than with the more resistant wild ones.

The causes of fluctuations in the populations of wild animals, such as the amount of food per individual and the presence of suitable living space available for them, together with other mortality factors, form a complicated system of interactions which demands study if it is to be properly understood. As in insect populations, however, apart from deaths which occur through senility, the greater part of the total mortality undoubtedly arises from biotic limiting factors. These consist, in large measure, of beasts and birds of prey. Fluctuations in animal populations are largely produced by fluctuations in those of the predatory animals which attack them. A scarcity of the latter will tend to result in an increase in the number of prey, provided that other conditions are favourable; whereas, an increase in the population of predatory animals will be followed by a corresponding decrease in the population of the prey and hence in the numbers of carcasses which they can provide.

Many of the predatory animals are also scavengers which utilize carrion as food. Among these is the jackal. Such animals not only reduce the number of potential carcasses by attacking the living prey, but also remove actual carcasses from circulation.

As an illustration of the relationship between two populations of animals, one of which devours the other, a report of Shelford (1931) on the increase of deer following the destruction of predatory animals by the early settlers of the State of Illinois may be cited. This destruction of wolves, foxes and wild cats resulted in a continuous decrease in their populations so that they became virtually exterminated. When the population of wolves had been reduced by approximately 50%, the deer multiplied rapidly for about 10 years and reached a population level which was three times as high as before.

In South Africa, it is undeniable that the blowfly position has steadily deteriorated during the last 20 or 30 years. This period roughly coincides with the rapid extension of sheep rearing over large tracts of country, but this fact does not provide the full explanation of blowfly increase. In the past, birds of prey and carnivorous animals formed a normal part of the wild fauna. Unfortunately, these predatory animals do not confine their attentions to the indigenous fauna but will also attack domesticated animals of a suitable size, such as fowls and lambs. Indeed, the habit of keeping these latter in flocks and herds renders them comparatively easy prey. In retaliation and in order to protect their livestock, farmers have consistently destroyed these predators by every means in their power until, at the present time, the jackal and vulture are comparatively rare in most sheep districts.

In thus solving the problem, however, other problems have been created or are being created. Almost unnoticed for many years, the gradual extermination of the jackal and the vulture was accompanied by an inevitable gradual increase of the many smaller, herbivorous denizens of the countryside. Mammals, birds and reptiles became emancipated from the constant threat of their ancient enemies and were enabled to breed more and more freely as time went on. Coupled with a relatively high reproduction potential, this unrestricted breeding has enabled the populations of the small animals to assume alarming proportions in some cases, and the total mass of living animals per unit area is to-day higher than it has ever been.

The dassie, mentioned above, is one of those animals which has thus become free to breed extensively. Since this increase in population means a greater number of carcasses per unit area per unit of time, a greater quantity of medium for blowfly development has become available. Thus, by the destruction of important natural checks to increase in dassie and other populations over large areas of country, the blowfly population has been indirectly encouraged. By solving one problem in a hasty but thorough manner, two others have been created in its place. These promise to prove costly and difficult to solve satisfactorily.

The above factors are ones that have no direct connexion with the blowfly population or its density. These factors control the amount of food which becomes available for maggots from time to time and hence control the intensity of competition which will occur. This plays a large part in determining the size of the fly population present at any one time.

2. *Location of available carrion*

A number of workers have observed that the distribution of adult flies over a given area is markedly irregular, as shown by trapping experiments. This seems to be due mainly to certain topographical features which produce an uneven incidence of optimum or near-optimum habitats for the flies.

Gurney & Woodhill (1926), in New South Wales, noted that blowflies were more abundant in timbered than in open country during periods of extreme heat or cold. They were also more numerous near permanent water in dry weather. In South Africa Smit & du Plessis (1926) recorded more flies from traps in damp, low-lying ground with good shelter than from those exposed. Smit (1931) says that *C. marginalis* is less strongly attracted to these damp, sheltered situations than are the other species. Traps situated along a river bank caught many more flies than those placed elsewhere. In Australia, Beveridge (1934) noted that strike in sheep was considerably higher among those animals which were in fields through which streams flowed than in those where only surface water in the form of ponds or in troughs occurred. He suggests that the larger fly population along the streams is correlated with the higher atmospheric humidity in these localities which leads to greater fly activity.

Finally, Parish & Cushing (1938), working in America, conclude that the density of shade, protection from direct wind, proximity to large ponds or running streams, the relative humidity of the atmosphere and, to some extent, the density of the surrounding timber and underbush appear to be the most influential factors which determine the numbers of the different species inhabiting particular locations.

There is thus a general agreement that the type of location governs the density and activity of fly populations. It follows that the location of a carcass within a given area will have a direct influence upon the extent to which it becomes used by blowflies for oviposition.

In places which most nearly approach the optimum habitat for adult activity, a carcass will be recipient of large numbers of eggs and will become crowded with maggots. Severe intra- and interspecific competition for food will result. In less favourable places, the carcass will be less crowded and competition will be correspondingly less intense. It is easy to see the probability of a gradation in habitats from those most favourable for fly activity to those which are definitely unfavourable within a given area. The degree of competition in a carcass will depend upon where, within this range of situations, the animal came to die, i.e. it will be purely a matter of chance.

The observation of Smit, quoted above, indicates the possibility of a specific attraction of each type of habitat for a particular species of fly. This would mean that the balance of the species in the adult population of flies is dependent upon the kind of habitat, and that the specific composition of the larval population on a carcass will depend largely upon its location. It has been shown that the outcome of interspecific competition among fly larvae is very largely a matter of which species are present in the mixed population. The location of carrion is therefore an important factor in determining the influence of competition on the general blowfly population.

3. *Suitability of carrion*

The association between the species of fly and the stage of decomposition of a carcass is well known. As Mackerras (1930) remarks, the environment which is suitable for the development of the larvae of a particular blowfly can no longer be considered as any carcass, but only those carcasses which are in a certain stage of decomposition. Each carcass is suitable for blowfly development for a strictly limited period, which will vary with the external factors which hasten or retard the process of disintegration. During warm weather, decomposition is rapid, and the stage at which primary flies are attracted is very quickly passed. Under these conditions, there will be very little or no oviposition by *Lucilia* or *C. chloropyga*, and the carcass will be inhabited mainly by the secondary group of flies. On the other hand, the temperatures during the winter months serve to retard decomposition, and the primary stage is prolonged so that the carcass becomes crowded with the progeny of the primary flies.

At this time the secondary flies have very little chance of gaining a footing on the carcass. This is the partial explanation of why a species like *C. albiceps*, which is present throughout the year, can only exist in small numbers on carrion during the winter in spite of its predatory habits. The primary species are able to devour most of the available food supply before the *C. albiceps* maggots commence feeding.

During the winter there may be a sharp difference in the suitability of the various kinds of carrion. According to Deonier (1940), the temperature of a carcass is considerably higher than that of the air. This is due partly to the amount of heat absorbed from the sun during the day but is principally accounted for by the heat which is generated by developing larvae in the carcass. Deonier records temperatures of 70° F above that of the atmosphere in certain parts of carcasses and of more than 50° F above in the larval masses. This generated heat enables the larvae to continue their development and the species to survive periods when weather conditions are unfavourable to adult activity.

This is generally true of large carcasses, but the dead bodies of smaller animals, such as rabbits, cats and lambs, are apparently unsuitable during winter, since the blowfly larvae on them are unable to generate and maintain the heat at a level sufficiently above that of the surrounding atmosphere to give rise to favourable conditions for continued development.

If this is generally true, then a further restriction of the available carrion, through the unsuitability of certain kinds of carcasses, occurs during the winter months. This conclusion cannot be applied to South African conditions without due allowance being made for climatic differences between this country and America. Such a restriction, if it takes place at all, must be limited to a comparatively brief period during the Karroo winter. It is non-existent in the warmer areas of the country. It may provide a partial explanation of the fact that, in the Karroo, the population of *Lucilia* is sometimes lower than might be expected from its obvious advantages over other species.

Since it touches the question of carcass suitability, the observation of Fuller regarding the apparent predilection of certain species of flies for the carcasses of certain kinds of animals, quoted earlier, also belongs here if confirmed. Such a deliberate exercise of choice would no doubt be ascribed to some suitable factor.

4. *Balance of species*

The number of eggs deposited on a carcass by each species of blowfly at any one time will obviously depend to a great extent upon the abundance of that species. This, apparently, is not the whole of the story. Mackerras & Mackerras (1944) emphasize the importance of the percentage of gravid females in a fly population with regard to the extent of oviposition. In the case of *L. cuprina*, the proportion of gravid flies was found to be generally low, being about 5% of the total fly population. At times this increased to 15% and once it rose to as much as 25%. Other conditions being favourable, the amount of oviposition on sheep and on baits depended upon the number of gravid females present. If this number were low, very little oviposition occurred either on the sheep or on the baits. The strike and bait infestation rose with an increase in the proportion of gravid females in the population. The bigger the population, therefore, the greater the amount of oviposition both on sheep and on carrion. These authors found that, both in the field and in the insectary, the degree of population density may be correlated absolutely with the number of susceptible areas found and with the total amount of oviposition. In the field, only some of the most attractive areas are found. These conclusions, although primarily referring to susceptible sheep, should also be applicable to attractive carrion.

If the above is accepted, the extent of breeding by a species on a carcass will depend very largely upon the density of the parent fly population in the area. Although the reproductive potential of a species may be comparatively high and, theoretically, a few individuals should be able to give rise to a noticeably large population of larvae, this capacity will be modified considerably by the proportion of flies which are gravid. This factor is influenced by events in the previous history of the population, such as the advent of suitable conditions for mating, the prior availability of the necessary protein meals, etc. Furthermore, there is a definite element of chance in the finding of suitable breeding places by the gravid females. The location of the available carrion in relation to the most favourable environment for blowfly abundance has also to be borne in mind, since the flies will be attracted to the environment first and will then encounter the carcass.

It is evident that the relative abundance and hence the balance between populations of the different blowflies is influenced very largely by seasonal and environmental factors. There will be times when the population of one species will be much greater within the unit area than is that of another belonging to the same seasonal group. It will therefore tend to deposit many more eggs on available carrion than will the less abundant species. Superficially, this would appear to give the first species an advantage in competition, so that the second species would suffer accordingly. This method of arguing from mass of population only has been used by certain observers in drawing some sweeping conclusions on these lines. It is pertinent to inquire whether this is so or not.

It has not yet been possible to carry out extensive tests on the question of balance of populations on carrion, but the following example will serve to show the danger of hasty judgement. A series of six replications in which 100 *Lucilia* and 500 *C. chloropyga* larvae were initially placed on a piece of beef of the standard size and weight (140 g.) gave the following results. The surviving population consisted of 224 *C. chloropyga* and 75 *Lucilia* adults. The total mortality in each population was 55 and 25% respectively. The *C. chloropyga* population consequently suffered a higher proportional loss than did the *Lucilia*, which reacted with a survival value approximately the same as was found in the case of pure cultures of the species at the same initial population mass. Putting the data into *Lucilia* equivalents in order to express them in terms of mass, the initial population of 768 gave rise to a final population of 374, giving a total mortality of approximately 51%.

This can be compared with the pure cultures of *Lucilia* and *C. chloropyga* and with the *Lucilia-C. chloropyga* series, taking the same initial population mass each time. The pure cultures of the two species showed 30 and 29% mortality respectively, while the mixed population gave a mortality of 29%. In these cases the total mortality was considerably less than in the present series. Furthermore, the excess mortality in the latter occurred entirely in the *C. chloropyga* population. The effect of increasing the proportion of *C. chloropyga* in the mixed population has been to decrease its survival value, while the less abundant *Lucilia* has remained unaffected.

The explanation of this appears to be along lines already put forward. The earlier-maturing *Lucilia* leave the remains of the food to *C. chloropyga* which then undergoes a more severe form of intraspecific competition than was the case in other series, since there are now proportionately more larvae of this species present. The deciding factor is therefore intra- and not interspecific competition.

Other things being equal, however, the more abundant species in an area will tend to occupy more of the available carrion than less abundant species, since it will discover more of it. It will, to some extent, be subject to less intense interspecific competition but more intense intraspecific competition than the less abundant species, since the latter will be absent from some of the carcasses located by the former. This is sometimes indicated by the results of carcass exposures. The question of the balance between the populations of the different species and its influence upon the degree of competition which occurs on carrion is more complex than appears at first sight. Further investigations on this aspect are required.

5. *Specific adaptability*

In the laboratory work it was found that certain inherent adaptations for withstanding the adverse conditions of competition were present in fly populations. These will influence the outcome of competition in the field. They are, in fact, among the most important of the factors which do so. The extent of this influence will vary with the species concerned.

The adaptability of species to ranges of temperature within which functional activity (i.e. oviposition and the like) can occur determines the minimum temperature at which a given species can deposit eggs. No special study has been made on these lines for South African blowflies, but it is known that this minimum temperature varies with different species in other countries. In America, Deonier (1940) records the following minimum ranges in which various flies become active about carrion: *Cynomyia cadaverina* R.-D., 40 to 50° F; *Phormia regina* Mg., 40 to 50° F; *Lucilia sericata* Mg., 50 to 55° F; and 50 to 60° F for certain species of *Sarcophaga*. It is probable that a bigger difference exists between some of the South African flies. From laboratory rearing, it is known that *C. marginalis*, for example, requires a much higher minimum temperature for egg-laying activities than does *Lucilia*. This is borne out by the field records. *Lucilia* is also active at a much lower temperature than is *C. albiceps*.

The reaction of flies to changes in atmospheric humidity is important, since it may also regulate oviposition. *C. albiceps*, for example, is influenced very appreciably by rainfall. A high rainfall during summer produces a rapid increase in its population; whereas a low rainfall results in a marked decrease. This may account, in some measure, for the very low winter population of *C. albiceps* in the Karroo. On the other hand, *Lucilia* breeds most readily on carrion during the winter months in all areas—when the rainfall is either high, as in the winter rainfall area, or non-existent as in the Karroo.

The adaptation of any or all of the species to an existence on food media other than carrion, at times when the latter is scarce, would tend to maintain their populations at a higher level than would otherwise be the case, and thus to increase competition on carcasses when these become readily available again. All the species are able to develop on living animals, although the extent to which they do so is limited. In the case of *Lucilia*, it is known that the maggots can develop in media other than flesh, e.g. in fowl manure (Illingworth 1923).

6. *Parasitism and predatorism*

Much discussion has appeared regarding the role played by parasites and predators in the control of blowfly populations. The conclusion favoured by Australian workers is that natural enemies reduce the intensity of competition between larval populations and, on the presumption that competition is the primary controlling factor, are disadvantageous (see Mackerras (1930) for a discussion of this). McCulloch (1942) sums up the general attitude by saying that parasites are not now expected to give control because the most promising ones have failed in the past and, anyhow, blowfly numbers are not kept down by parasites anywhere in the world.

It is to be hoped that a satisfactory account of parasitism and predatorism in blowfly populations will become available. As far as the present writer is aware, no proper attempt has yet been made to assess the value of parasites in blowfly control, nor has any attempt been made to discover just why parasites and other natural enemies do not succeed in limiting blowflies sufficiently to prevent their becoming an economic problem.

There is no question that parasites and predators do influence competition between blowfly larvae. It would be surprising if this were not the case. So far, however, only the obvious reduction of adult populations and the consequent decrease of the competition (when it occurs) in the larvae of the ensuing generation has been emphasized. There is an even more important aspect which has a profound effect upon the general balance of populations.

The habits of the different species of flies are of first importance, since they determine the degree of accessibility of the immature fly population to the natural enemies. In South Africa, the latter comprise at least five different species of hymenopterous parasites, some of which attack the larvae and others the pupae. There are also a number of Staphylinid and other predacious beetles as well as birds and possibly other animals. Accessibility to parasite attack is governed largely by the length of the larval feeding period and by the pupation habits. Both of these vary widely in the different species.

On carrion, *C. albiceps* is the most accessible, and normally suffers a high degree of mortality through parasitism and the depredations of the various beetles. This probably accounts for the low population throughout the year as compared with other species. The remaining *Chrysomyia* species are less susceptible but are more so than *Lucilia*. Since *C. albiceps* usually reaches its maximum at the same time as *C. marginalis*, it might be expected to control this species except for the lower population which it produces at this time.

Lucilia is the least affected by parasitism, since this mainly occurs during the pupal stage of the fly and pupation is largely in situations which are inaccessible to the main pupal parasite, *Mormoniella vitripennis*. Having a shorter larval feeding period than any of the other species, it is also less liable to attack by larval parasites, although it is most vulnerable during this stage.

The action of predators in reducing the immature fly population will be similarly affected by the inaccessibility of a certain proportion of the population. The final result of the work of parasites and predators will therefore depend largely upon the proportion of the host population which pupates in protected situations. Since the blowfly species vary widely in this respect, there will be a differential mortality between the species. In this, the primary flies are favoured. In particular, *Lucilia* very largely escapes attack. The secondary flies are more prone to suffer heavy parasitism, since they are always more exposed during the pre-imaginal cycle. *C. albiceps* suffers more severely than any other fly. Thus, the population of a fly which might be expected to exhibit a high potential for the destruction of other larvae which occupy the same piece of carrion is reduced to such an extent that it cannot reproduce in the field the highly successful control observed in the laboratory.

Parasitism and predatorism therefore tend to alter the balance between the adult fly populations and hence to regulate the relative numbers of eggs laid by each species on the available carrion. In this way, the degree of interspecific competition is modified, although the intensity of competition as a whole may not be reduced.

XI. Competition as a factor limiting blowfly populations

1. *Food supply and population growth*

As a primary basis for discussion, it can be assumed that, within a given unit area, the amount of consumable carrion which is both suitable and available for the development of blowfly larvae is strictly limited and remains approximately constant at all times. This will support a given number of larvae of a given size and hence can give rise to a certain maximum fixed population mass. The population of flies within the area will tend to increase to a maximum, and this growth in population density will take place in approximate accordance with the well-known Verhulst-Pearl law of growth, provided that no other factor intervenes. This type of growth occurred in the laboratory populations. Beyond the asymptotic maximum, increase in the initial population means a marked increase in total mortality so that the curve descends rapidly to, or very near, zero.

From the field records (see figure 47) it is clear that something very similar to the laboratory events occurs in nature. This is particularly evident in the case of *Lucilia* and *C. chloropyga*. The populations of flies increase in density until the universe represented by the available carrion is fully occupied. The manner in which they do so is in close conformity with the normal growth law. After this stage, further contributions of progeny by the rapidly accumulating population of adult flies result in suddenly increased mortality and a rapid decline in the number of survivors in place of the previous increase.

The amount of food (i.e. of carrion) which is available within a given area therefore determines the *maximum* potential population of flies which can be produced within that area, but it does not determine the *actual* density of the population produced. Thus although it may be regarded as the primary factor limiting blowfly abundance, other factors combine to regulate the numbers of flies which can emerge from a given carcass. Some of these factors have been enumerated.

In nature, the available carrion is nearly always crowded with fly maggots, and some measure of competition for the food supply is nearly always present. Mackerras (1930) remarks that the uniformity with which competition is observed makes certain that the blowfly population is always greatly in excess of the numbers that would be required to find and occupy all the available carrion. While this may be true—and in some cases it seems likely that the overcrowding of a carcass might be so severe that the resulting competition will even produce the death of all the individuals thereon (see the laboratory results)—the problem can be stated in the reverse manner.

The fact that there is always a large population of blowflies in the field goes to show that there is sufficient food in the environment to produce this excessive population in spite of the overcrowding and consequent competition on carcasses. If competition is regarded as meaning the result of an unfavourable ratio between the amount of food available and the density of the adult fly population within a given area, then it is evident that the conditions are not sufficiently unfavourable at the present time to serve as a successful factor in producing an 'economic control' of blowfly populations.

That this is due to a gradual increase in the amount of food which is available in the field seems likely. The reasons for this belief have been given. Any attempt at a restoration of a previous balance by means of the destruction of carcasses when discovered would seem to have little hope of achieving any great measure of success. Such a method would deal with a relatively small proportion of the carrion present and would consequently have little effect upon the general fly population in the field.

2. *Competition and population density*

A number of workers have laid stress on the great reduction in fly populations by competition and on the part parasitism plays in rendering competition less effective. The fact has apparently been overlooked that competition, by itself, cannot result in a stabilized fly population, and that the outcome of competition itself produces the phenomenon attributed to parasitism.

Intense competition, in reducing the survival value of a larval population, gives rise to a small population of flies which are probably below average size. These will lay comparatively few eggs, so that the carrion they find will be less crowded with their progeny. Little competition will occur, so that the final population of flies will be larger than that of their parents. More eggs will therefore be deposited on carrion. This increase of progeny will continue until the adult fly population becomes sufficiently abundant to produce intense competition once again and so to give rise to a corresponding sudden decline in the number of flies emerging. Hence, competition will tend to result in somewhat violent fluctuations in population density over a period of years and, were it left to itself, it would be most likely to give rise to periodical outbreaks which could be very much worse than anything now known.

The situation in South Africa appears to be that of competition which is only slightly tempered by parasitism and other factors. It is to be noted that the farmer speaks of 'bad fly seasons', indicating that recurrent high peaks of population density such as those mentioned above are actually taking place. The carcass records illustrated in figure 46 show this more convincingly. The populations of *Lucilia* and *C. chloropyga* were higher during the winter of 1941 than in 1942 and the summer of 1941 to 1942 was a 'bad fly season', whereas, during the 1942 to 1943 summer, strike in sheep was less prevalent.

3. *Modification of competition*

Some of the main factors which tend to modify the intensity of competition in nature have been dealt with earlier in this paper. The two which probably have the greatest effect are the specific reactions of the flies and the extent of parasitism. Since the primary flies are the ones which are of importance from a practical point of view, it is proposed to deal with these here.

It has been shown that, under conditions of straightforward competition, the main primary fly (*Lucilia*) is very well adapted to withstand adverse conditions of overcrowding. In this it compares more than favourably with all the other species, and its description by Fuller (1934, p. 54) as a 'comparatively inferior species' is the reverse of the truth. It is also the least susceptible to parasitism, both by reason of its habits and because it occurs on carrion mainly during the winter when parasites are not very active.

Parasitism is said to be disadvantageous because it reduces competition and therefore tends to the ultimate production of larger populations of flies. This statement is not supported by any exact data as far as the present writer is aware. It cannot be accepted unconditionally as a general rule, even from *a priori* considerations. *Lucilia* and *C. chloropyga* populations very largely escape parasitism during their main breeding season, yet they are very much more abundant than *C. albiceps*, which is particularly prone to attack.

Both parasites and predators must tend to damp the violence of the fluctuations in fly populations produced by competition. The attack of natural enemies will be most intense at times of maximum blowfly abundance, i.e. when there is an exceptionally favourable host density. They will therefore serve to reduce the emerging population of flies and so to reduce the ill-effects of competition.

The same may be said of predators of the adult flies. Ullyett & de Vries (1940) have shown that *Bembix* wasps use blowflies as prey only during those periods when flies of these species are among the most abundant dipterous insects in the field.

The effect of parasites and predators will therefore be to tend to stabilize the population density of blowflies and, on this view, natural enemies are a necessary adjunct to competition in controlling flies in nature.

4. *Conclusion*

It will be appreciated that a great deal more must be known of the relationships between competition for food and other controlling factors in blowfly populations before a true assessment of their places in the general limitation of fly populations can be made. The investigation, so far, has shown that it is not possible to solve the problems involved by theorizing. Neither can the results of casual observation be relied upon to provide answers to any parts of the general problem. Exact experimental data are necessary.

From field observations it would appear that, while competition for food is the basic factor limiting blowfly abundance, it does not serve to maintain these populations below the level at which they constitute an economic menace. It is suggested that an improvement in the ratio of food supply to fly population per unit area within comparatively recent years, due to the disturbance of the natural balance in sheep-rearing areas, is the primary cause of the gradual increase in blowfly abundance. This has not been accompanied by any material increase in the other natural mortality factors in the populations of flies themselves, and there has therefore been no compensating factor for the increase in food.

A number of factors combine to render competition relatively ineffective as a practical controlling factor for the important primary species of blowflies. The most important of these are summarized here.

(1) The ability of the fly population to adjust itself to a shortage of food. This inherent property is strictly limited and varies in extent with the species concerned. It has been shown that this adaptation to adverse conditions depends upon (*a*) a reduction in the size of the individuals in a population to the minimum size for the species which is compatible with the production of viable pupae; (*b*) the relative rate of larval growth; (*c*) the relative minimum food requirements per individual; (*d*) the relationship between the size of a fly and its fecundity.

Lucilia, which is economically the most important of the flies, makes use of these adaptations to the highest degree. It is therefore the most successful of the flies when faced with intra- or interspecific competition. It has the great initial advantage of having the smallest larva and is therefore able to maintain a larger population on a given amount of carrion than are the other species. *C. chloropyga*, which is also a primary fly, follows *Lucilia* in these advantages.

(2) The seasonal grouping of flies. This has the effect of reducing interspecific competition very considerably. It also separates the primary from the secondary flies. There is therefore little or no major competition between these two groups. As the secondary flies include *C. albiceps* which is unique in that it is predatory in habits, reduction of primaries by its action is practically non-existent. Competition therefore occurs mainly between flies of the same group and *Lucilia*, which is markedly superior to *C. chloropyga*, is able to maintain

a normally higher population than would be the case under conditions of fourfold competition. It is quite clear that *C. marginalis* plays no important part in limiting the populations of primary flies.

(3) The suitability of carrion as determined by climatic factors is largely responsible for this grouping. During winter, the carrion remains attractive to primary flies over long periods and hence provides the opportunity for large numbers of flies to develop. Nothing is known as to the relative abundance of carrion during summer and winter seasons, but it is probable that the severity of the Karroo winters causes a greater proportion of deaths among animals than occurs during summer, so that it is likely that more food is available during that season.

(4) The fluctuating nature of the food supply will have a distinct bearing upon competition. Nothing is known about the variation in numbers of carcasses during the course of any one year or from year to year. This is probably not great. The evidence points to a steadily increasing supply of carcasses at the present time rather than to fluctuations. This means that less competition is taking place and therefore that the general level of the fly population will continue to rise until the populations of animals from which carcasses are derived reach a saturation point.

(5) Climatic influences play a part, not only in affecting the quantity of suitable food at any given time but also in affecting the fly population itself in two ways. In the first place, the atmospheric humidity and temperature will tend to influence the proportion of gravid females in the population and thus to limit the number of parent flies. In the second place, temperature and humidity have an effect upon activity of flies. Both resultants determine the extent of oviposition and hence the degree of competition on carrion. It is well known that a year of high rainfall is marked by a noticeable increase in fly activities and in incidence of strike, although the latter is due to the effect of rain on the increase of susceptibility of sheep.

From the conclusions to be drawn from the present investigations which, in some cases, agree with those of previous workers but in others do not, it is evident that it cannot be left to competition to reduce fly populations to a point where they no longer constitute a nuisance. As pointed out by Mackerras (1930), there is always a surplus of flies in nature over and above that number which would be required to find and occupy all available carrion, and it is this surplus that must be destroyed before the population can be reduced to a point at which the larvae no longer fill their environment, i.e. at which some degree of control proper is attained. It would seem, from the available evidence, that sheep are less attractive than carrion. The reduction of the surplus population of flies to the extent indicated might therefore reduce the incidence of strike to insignificant proportions.

It is to means of reducing populations other than by competition that we must turn in order to try to obtain a solution to the blowfly problem if we are to attack it directly. At present, resort is had to temporary palliatives in the form of dressings to render animals less attractive to the flies. There is also the more permanent Mule's operation. Both involve expense, and the former is a method which entails regular and careful attention throughout the season. Permanent methods are required, and two avenues of approach immediately suggest themselves. The most obvious and promising is the development of a breed of sheep that will be less susceptible to blowfly attack. This can be done without the sacrifice of any of the wool-producing qualities of the breeds at present used. The second method is by a direct attack upon the blowfly population itself.

It is too early to say what hopes of success exist for the second of these methods. We require to know a great deal more about the relationship between blowflies and their environments before an answer to many of the questions involved can be given. It is hoped that work now going forward will add to our very inadequate knowledge of this aspect of insect control.

XII. SUMMARY

1. The investigations described in the present paper form part of a more comprehensive programme of work on the natural control of sheep blowflies in South Africa. This has been undertaken by the Parasite Laboratory, Pretoria as a long-term project which will include both field and laboratory studies. Competition for food among larval populations forms the background of all natural control of the flies, since the primary factor which limits the abundance of any population of insects is the quantity of food which is available to it within its given universe.

2. Five species of blowflies occur on carrion in this country, viz. *Lucilia sericata* Mg., *L. cuprina* Wied., *Chrysomyia chloropyga* Wied., *C. albiceps* Wied. and *C. marginalis* Wied. Of these, *C. marginalis* is the only one which is not directly concerned in strike in the living animal. There is some doubt as to the authenticity of *L. cuprina* as a separate species, and it is thought to be a form or race of *L. sericata*, with which it agrees in its general behaviour.

3. The normal larval growth of each of the above species was studied. It was observed that *Lucilia*, by its smaller maximum growth weight and hence the smaller quantity of food required for full development, as well as its more rapid and earlier development on carrion, has a distinct advantage over all the other species in the acquisition of food.

4. This advantage was evident in experimental series in which the effect of varying degrees of both intra- and interspecific competition for food was tested with the various species of blowflies in the laboratory. With the exception of *C. albiceps*, *Lucilia* exhibited a superiority in survival value over all other species. *C. albiceps*, by reason of its predatory habits, is able materially to reduce larval populations of other species associated with it on carrion and to increase its survival value thereby. The reasons for the relative survival value of the different species are discussed and shown to be inherent in the method of growth of the species.

5. It is shown that *C. marginalis*, although it occurs very commonly on carrion in summer and is the largest of the species, cannot and does not control populations of primary flies when these occur in association with it.

6. Competition affects the fecundity of flies from larval populations which suffer from it. The effect produced varies in direct proportion to the intensity of competition, the most intense competition producing very small flies which can lay few eggs. In this respect, *Lucilia* suffers less than other species.

7. In all species, the first reaction of the larval population to competition is to effect a reduction in the average size of the individuals. They thus sacrifice size in favour of numbers. There is a minimum size below which viable pupae cannot be formed, so that the extent of this adaptation to food shortage is limited by the absolute minimum size for the species. Total mortality increases at the same time as the reduction in size is proceeding.

8. Field records show that blowflies may be divided into two seasonal groups, viz. summer and winter breeders. These two groups coincide with the classification into secondary and primary flies respectively. It is shown that interspecific competition is mainly confined to species within the same seasonal group. Secondary flies therefore cannot materially influence the general population of primary flies. Overlapping between the groups and the consequent three- or fourfold competition occurs only for a short period in autumn and spring. *Lucilia* comes into conflict mainly with *C. chloropyga* and, as was shown in the laboratory populations, the result is one of intensified intraspecific competition within the population mass, with *Lucilia* holding the advantage in actual numbers of survivors.

9. Competition is treated generally in the light of the available field data. The latter is shown to be deficient for the present purpose. The availability of carrion, which is the main limiting factor, is shown to be dependent upon factors outside the blowfly population, and some of these factors are discussed. Reasons for believing that the quantity of available carrion has increased within recent years in the main sheep-producing areas are given. This increase in carrion would account for the marked increase in the general fly population which has undoubtedly occurred. It is traced to the disturbance of natural balance by man.

10. Competition, while it tends to limit blowfly populations in nature, also tends to produce violent fluctuations in fly abundance. This gives rise to periodicity of outbreaks and is the cause of the 'bad fly seasons' known to the farmer. Natural enemies of blowflies tend to damp these fluctuations but are not numerous enough to produce much effect at present.

11. As a controlling agent, competition does not serve to give results which are economically satisfactory. It is obvious that a heavy surplus is always present in the field, and that there is always enough available carrion to maintain this surplus. The reduction of food by the destruction of carcasses in the field, while sound in principle, does not promise to be successful in practice since the number of carcasses which will be found will undoubtedly represent a very small proportion of the total number present within the area.

12. Before any control measure which uses natural control factors can be envisaged, we require to know a great deal more about the relationship between the population of flies and the whole of their environment, as well as about factors which influence competition in the field.

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Thirty tables of data have been deposited in MS. in the Library of the Royal Society where they may be consulted by workers in this field. Facilities for obtaining photostat copies of the tables are available.

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