EVALUATION OF SOME OF THE FACTORS INVOLVED IN ECOLOGICAL SUCCESSION IN AN INSECT POPULATION BREEDING IN STORED WHEAT

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INTRODUCTION

In an earlier paper (Coombs & Woodroffe 1963a) we described an experiment demonstrating ecological succession in an ecosystem comprising stored wheat infested by several species of insects. During the first two years of the experiment the grain weevil, *Sitophilus granarius* (L.), was the dominant species. It then died out and the Australian spider beetle, *Ptinus tectus* Boield., increased in numbers and predominated for the next three years. Subsequently the population of *P. tectus* declined and the fur beetle, *Attagenus pellio* (L.), became the only surviving species.

This succession differed in two respects from most other described instances of succession in animal communities. Firstly, it took place in a closed system in which no immigration or emigration could occur. Consequently all species were present from the beginning of the experiment and the species which predominated in the later stages had survived the earlier, less favourable, conditions; they did not gain access only when the conditions became suitable. Secondly, the environmental changes (the conversion of whole wheat into husk, frass and dead insects) which formed an integral part of succession were caused by the insects and not by a successional change in fungi or other organisms, nor by some external factor such as weather.

We suggested previously (Coombs & Woodroffe 1963a) that the observed succession might be the direct result of differing rates of increase of the species under the physical conditions of the experiment, but pointed out also that an interaction between *Sitophilus granarius* and *Ptinus tectus* which we had already studied (Coombs & Woodroffe 1962) led us to believe that the full explanation of the succession was more complicated. We also suspected that causes other than the physical environment were involved when we compared the ambient temperatures recorded over the duration of the experiment (Fig. 1) with the observed numbers of *P. tectus* adults (Fig. 4). The latter increased over the first two years, fell during the third and increased again in the fourth year. Had temperature been a limiting factor, the population would have increased more during the warm third summer than during the second or fourth.

Further work (Coombs & Woodroffe 1965, 1970) demonstrated a series of interactions between *Sitophilus granarius* and *Ptinus tectus* that influenced the rate of increase of the latter. These interactions were studied individually by means of small-scale laboratory experiments and because of this the results cannot be used to compare the relative importance of the different interactions in determining the course or timing of the succession.

In the present paper estimates of the potential performance of *Sitophilus granarius* and
\[ \textit{Ptinus tectus} \] when breeding separately, but otherwise under the conditions of the experiment, are made and compared with the values observed in the experiment. The parameters used in the computation of the estimated performances are then manipulated in a manner and at a time which our experiments suggest to be realistic, in order to determine what changes in value of these parameters is necessary to make the estimated values consistent with the experimental observations. The original experiment was carried out in duplicate and the two sets of observations differed somewhat. Consequently, precise agreement between the observed and calculated population curves has not been sought and both sets of data are given rather than the mean.

HABITS OF THE SPECIES

The following brief summaries give biological data on the three species which are relevant to an understanding of the succession.

\textit{Sitophilus granarius} requires whole grain for breeding and the wheat grain normally supports the development of only one adult at a time. Females prefer to lay eggs in intact grains but, when these are scarce, grains from which an adult has already emerged may be used; relatively few such eggs produce additional adults. All developmental stages are passed within the grain and are thus protected from disturbance or predation by \textit{Ptinus tectus}. Grain supporting a breeding population is gradually converted into husk, frass (mostly faecal pellets), remnants of endosperm and dead insects. At 20°C and 60% R.H., adults live for about 250 days and lay about 125 eggs (Eastham & McCully 1943) and complete development (egg to adult) takes about 60 days; the developmental period increases to about 160 days at 15°C (Eastham & Segrove 1947).

\textit{P. tectus} will breed on material of both animal and vegetable origin and favours finely divided foodstuffs (Howe 1949). All stages occur more or less freely in the food medium, though the feeding larva produces a loose cocoon of its own faecal pellets and, when fully grown, spins a tough silken cocoon for pupation. The adult lives for about 220 days at 20°C on wheatfeed when given drinking water but for only about 65 days without water. Fecundity is about 420 eggs/female when drinking water is provided but is very low (less than 10 eggs/female) without it. Complete development on wheatfeed takes about 80 days at 20°C and 70% R.H. (data from Howe & Burges (1953) except for fecundity without water which are our own).

\textit{Attagenus pellio} will breed on both animal and vegetable materials, but development is faster on the former. All stages occur freely in the food medium. The adults fly, and are also found on flowers where they feed on nectar and pollen. They may pass the winter in diapause, but otherwise live only a few weeks. At 20°C and 70% R.H., on a food of fishmeal, yeast and cholesterol, development takes 1, 2 or 3 years while on wholewheat flour it takes 3 or more years. The developmental period on \textit{Sitophilus} frass is similar to that on fishmeal.

PREDICTION OF CHANGES IN NUMBERS OF \textit{SITOPHILUS GRANARIUS} AND \textit{PTINUS TECTUS} USING BASIC DATA

(1) Based on the intrinsic rate of natural increase

Birch (1948) defined the intrinsic rate of natural increase \((r)\) as 'rate per head under specified physical conditions, in an unlimited environment where the effects of increasing density do not need to be considered'. It has been used to predict which of a group of
species is likely to predominate in a mixed population (Birch 1948; Howe 1953). In spite of the fact that our experimental population was not in an unlimited environment, nor was it likely to achieve a stable age distribution (Lefkovitch 1962), the use of $r$ provides some indication of the potential of the two species at the temperatures experienced.

Andersen (1963) has published rough estimates of $r$ for Sitophilus granarius at 17, 21 and 25° C (70% R.H.) using an assumed survival from egg to adult of either 25–30% or 75%. Howe (1953) gives values for Ptinus tectus when free from competition at 15, 20, 23 and 25° C and for groups experiencing some intraspecific competition at 13, 20, 25 and 27° C. Comparison of the two species on the basis of these data shows clearly that $P. \text{tectus}$ has a greater potential for increase than Sitophilus granarius at temperatures below 20° C, even if Andersen's higher and Howe's lower values are used. The thermal conditions during our experiment (Fig. 1), which rarely exceeded 20° C, would thus favour

![Fig. 1. Mean weekly ambient temperatures during experimental period. ——, Year 1; · · · · , year 2; - - -, year 3; - - -, year 4.](image)

*Ptinus tectus*. However, Howe used an optimal food (wheatfeed) and supplied drinking water in his experiments while in our work the food was wheat and the only water which may have been available was in the form of condensation which appeared at one time on the glass sides of the containers. The potential rate of increase of $P. \text{tectus}$ in our experiment would therefore be lower than an estimate based upon Howe's data. Thus at 23° C, 70% R.H., the larval developmental period is 36 days on wheatfeed but about 70 days on wheat. Lack of drinking water affects adult longevity and fecundity. Howe & Burges (1953) showed that the egg production per female per week of a group of adults provided with drinking water at 20° C starts at over fifteen and falls gradually and evenly to two in the fiftieth week. In our experiments, also at 20° C but without drinking water (Coombs & Woodroffe 1965), oviposition occurred only during the first three weeks, at 3–4 eggs per female in the first week, 2–3 in the second and 0–1 in the third. In view of these results, it seems unlikely that the potential increase of $P. \text{tectus}$ exceeded that of Sitophilus granarius during the early part of the succession experiment except when the temperature was near or below the developmental threshold for $S. \text{granarius}$, which is higher than that for $Ptinus \text{tectus}$. 
Andersen's (1963) values of $r$ for *Sitophilus granarius* are more relevant to our experimental results than are Howe's (1953) data for *Ptinus tectus* because the former, but not the latter, used wheat as the food in his experiments. However, in our succession experiment the maximum population of *Sitophilus granarius* was predetermined by the number of wheat grains present. We can therefore expect agreement between the observed and the calculated figures only early in the experiment. The calculated values plotted in Fig. 2 were obtained by multiplying the number of adults present at the beginning of each week by the value of $\lambda$ (the natural antilogarithm of $r$) appropriate to the temperature. The resultant graph assumes a constant age distribution and represents the calculated number of adults present at any time. However, no introduction was made of the requisite number of eggs, larvae and pupae to provide a stable age basis for the initial thirty adults, so a calculation based on $r$ will considerably overestimate the initial increase. The calculated curve therefore overestimates the first generation (Fig. 2).

![Graph](image)

**Fig. 2.** *Sitophilus granarius.* Mean observed numbers (· · · ·) and numbers calculated using $r$ (——).

To correct this obvious error, the calculated curve has been made to coincide with the observed curve at week 48, when the first adults of the new generation appeared and when, as has been argued above, the two are most likely to agree. Following this adjustment, the curves are very similar. This is rather surprising because, although all stages would be present, by week 80, when the second peak of numbers was recorded, almost all the wheat grains would have been utilized.

It is noteworthy that, in spite of the assumptions necessarily made in calculating $r$ which were not true of our experiment, the parameter nevertheless makes possible a reasonable prediction of numbers in the case of *S. granarius*, though this agreement could be coincidental.

(2) Based on an empirical, step-by-step calculation

Since published $r$ values for *S. granarius* and *Ptinus tectus* proved inadequate for calculating the potential performance of each species under our experimental conditions, an alternative method was used. This necessarily involved making some assumptions which
are referred to under the appropriate heading. A general assumption throughout the following procedure is that the rate of development of the immature stages at any temperature can be expressed as the reciprocal of the average total developmental period of these stages at that temperature. It follows from this that a period at this temperature can be expressed as a percentage of the developmental period and it is assumed that these percentages for different temperatures are additive. This assumption has been shown to give a reasonable approximation to developmental period in the related *Sitophilus oryzae* (L.) (Anon. 1963). A similar assumption is made in respect of the pre-oviposition, oviposition and post-oviposition periods.

In general, basic life-history data were obtained from published information, but some experiments were carried out, especially on *Ptinus tectus*, to provide data not available in the literature. Sometimes extrapolation from inadequate data was necessary, especially to cover the lower temperatures experienced by our experimental populations. Since both species are known to be cold-hardy, and no extremely low temperatures were experienced, it is assumed that no deaths were directly attributable to low temperatures.

The calculations for *Sitophilus granarius* were carried out by assembling data, week by week, in columns A–P as follows.

(A) **Average air temperature for the week**

Temperature was recorded continuously alongside the experimental containers and since the experimental bulks of wheat were small, the average recorded temperature is regarded as approximating to the grain temperature. Change of temperature due to insect activity is considered later.

(B) **Number of ovipositing females**

For the first entry it is assumed that half of the introduced adults are females at the start of their oviposition period. Later entries into this column were completed by adding to the number of ovipositing females present at the beginning of the week half the number of adults completing the pre-oviposition period (column K) during the previous week and subtracting the number of females completing their oviposition period (column L) during the week.

(C) **Eggs per female per week**

It is assumed that the oviposition rate is determined solely by temperature and that so long as the female is laying it is unaffected by her age. The figures were obtained from published data and were corrected for developmental mortality by multiplying by 0.75 (the mean mortality for all data in Richards (1947) was 21.8%).

(D) **Total eggs per week**

The product of columns B and C.

(E) **Total life inside grains**

Each entry in this column represents the total of all previous entries in column D (effective oviposition) minus the total of all entries in column N (adults emerging).

(F) **Number of intact grains**

The number of wheat grains at the beginning of the experiment was estimated by weigh-
ing several samples and counting the grains. From this estimate was subtracted the number of emerging adults (column N), each representing an empty grain.

(G) *Life per intact grain*

Column E divided by column F.

(H) *Amended effective natality*

It is assumed that *S. granarius* requires whole grains to complete its development and that it is rare for more than one adult at a time to be produced from one wheat grain. The effective natality will therefore equal the number of grains utilized and as eggs are laid at random in a random selection of wheat (Richards 1947; Coombs 1956) the number of grains used can be calculated using the Poisson distribution and the mean life per grain (from column G). By using this measure, the effect of the limited food supply is, to a large extent, taken into consideration. It is possible that no adult would be produced from some grains containing more than one egg and in this calculation this has arbitrarily been taken to cancel the slight tendency for ovipositing females to avoid grain containing fourth instar larvae (Richards 1947) and the occasional additional adult emerging from some grains.

(J) *Percentage development*

This column is bipartite. In the first part the percentage development appropriate to the temperature in column A is entered. In the second these percentages are accumulated until 100 is reached or exceeded, which signifies that the eggs laid in the first week contributing to the 100 have become emerged adults. This number is transferred to column K (pre-oviposition) and N (adults emerged) and the percentage development attributable to the first contributing week is subtracted from the cumulative total. This process is repeated each time the accumulated total reaches 100. Any value over 99 was counted as 100 and in cases where 100 was exceeded all emergences were taken as occurring in that week.

(K) *Percentage pre-oviposition period*

This also is bipartite and compilation is as for column J except that the first entry is made on the emergence of adults. On completion of the pre-oviposition period, half the numbers of adults are added to column B (number of ovipositing females) and a note is made in column L that their oviposition period has started.

(L) *Percentage of oviposition period*

Similar to column K but, on completion, adult numbers are subtracted from column B (oviposing females) and calculation of their post-oviposition period (column M) is started.

(M) *Percentage of post-oviposition period*

Similar to column L, but on completion twice the number of adults is transferred to column O.

(N) *Number of adults emerging*

Entries are made after the completion of development.
(O) Number of adults dying
Entries are made after completion of the post-oviposition period for females, males being assumed to live equally long.

(P) Total number of living adults
This is completed by adding column N and subtracting column O from the numbers introduced at the start of the experiment.

The numbers calculated in this way and those observed experimentally are presented in Fig. 3. As in the curve based upon ‘r’, the effects of winter and summer temperatures are shown by the periods of stability and of increase of adult numbers. The improve-

![Fig. 3. *Sitophilus granarius*. Observed numbers (---: , dup. 1; ---: , dup. 2) and numbers calculated using weekly step-by-step method (---).](image)

ment of this over the previous estimate is mainly due to the allowance made for the finite experimental environment. Discrepancies remain, however, in that the calculated population increases more slowly to its second and final peak, its decline is less precipitous and, if allowance is made for the fact that the numbers are plotted logarithmically, the peaks achieved are higher than in our experimental population.

Data for *Ptinus tectus* were treated similarly. The information available in the literature mostly concerns adults provided with drinking water so it was necessary to carry out experiments to obtain data for adults denied water (Coombs & Woodroffe 1965). Also, as details of development with wheat as food were available for only two temperatures (both over 20°C) estimates of the values for temperatures below 20°C were made by making appropriate proportionate corrections to the figures for wheatfeed given by Howe & Burges (1953). The calculations (unlike those for *Sitophilus granarius*) took no account of density effects or food shortage, since *Ptinus tectus* does not require whole wheat grains for development, and a period for complete development consisting of the sum of the egg, larval, pupal and pre-ovipositional adult periods was adopted to permit maximum use of published information. Adults are thus regarded as emerging later than in reality but starting to lay eggs immediately. Because the number of adults present
in any one week is partly dependent upon length of adult life and this method of calculation shortens adult life, the calculated numbers of adults are slightly low. Developmental mortality was assumed to be 20% at all temperatures.

Comparison of observed and calculated curves of adult numbers (Fig. 4) shows reasonable agreement between them except that, as would be expected since food shortage was not taken into consideration, the calculated population continues to increase. Apart from this, the most obvious point of disagreement is in the period 110–140 weeks, when there was a much greater fall in numbers in the observed than in the calculated populations; the former subsequently recovered.

![Fig. 4. *Ptinus tectus*. Observed numbers (·····○, dup. 1; ·····×, dup. 2) and numbers calculated using weekly step-by-step method (——).](image)

**MODIFICATIONS OF BASIC DATA AFFECTING NUMBERS OF *SITOPHILUS GRANARIUS***

(1) Incorporation of effects of metabolic heating

Throughout the experiment the ambient temperature was recorded continuously by a thermograph, and so far this has been assumed to correspond to the temperature of the wheat. However, at high densities the metabolic heat produced by large numbers of insects in an insulating medium may cause a rise in the temperature of that medium. Such a rise was observed but not recorded during the experiment and thus the temperatures used to compile column A in the above calculations require correction. For this purpose it is assumed that a steady temperature state had been reached, so that the bulk of wheat could be regarded as an infinite slab 8 cm deep, with the surfaces at the ambient temperature. The rise in temperature at any point \( \theta \) is given by

\[
\theta = \frac{R(l^2 - x^2)}{2K}
\]

where \( R \) = rate of heat production, \( l \) = half depth of wheat, \( x \) = distance of measured point from half depth, \( K \) = thermal conductivity (from Robertson 1948).

When calculating \( R \), oxygen consumption given by Birch (1947) for *S. oryzae* was used and (following Howe 1962) was converted to gram calories of heat. Since a general figure for the whole bulk was required, \( x \) was taken at 2.5 cm, the temperature at this point being mid-way between \( l \) and the ambient. The temperature rise caused by 1000
adults was calculated for various temperatures and a similar value for stages inside the grain. (According to Birch (1947) the mean oxygen consumption of all stages inside grain is approximately twice that of an adult.)

A division into adult and pre-adult stages is necessary because the effect of metabolic heating was to increase temperatures from about week 60 until the population declined and this includes the period when no further grains were available for development. The temperature rise varied from about 0.5° C at week 60 to 10° C at about week 80 and then declined again.

The temperature increments calculated in this way are added to the temperatures given in column A and the whole set of subsequent calculations repeated. As before, the temperature is assumed to remain at one level throughout one week and then change abruptly to a new level for the next week.

![Graph](image)

**Fig. 5.** *Sitophilus granarius.* Observed numbers (· · · · ○, dup. 1; · · · · ×, dup. 2) and numbers calculated (---) using ambient temperature (A), temperature adjusted for metabolic heating (B). C1 and C2 adjusted for shortened adult life; C1 shortened to 50%; C2 shortened to 25%.

In Fig. 5 the experimental curves are presented together with the calculated curve as now modified (curve B). The collapse to zero now occurs some 20 weeks sooner and the rise to the final peak is more rapid than in the previously calculated curve A but this increase still occurs later than the average of the two experimental populations and the final peak numbers are approximately twice as high. It seems likely that the calculated development prior to the second major rise in numbers has been underestimated. During this period (week 16 to week 48) the mean temperatures used in the calculations were below 15° C and thus close to or below the minimum for development. At such a temperature the daily fluctuations about the mean would allow more development than would a period continuously at the mean (Richards 1959), and this might lead to an underestimate of developmental period.

(2) Effects of interspecific interactions

Since the developmental stages of *S. granarius* occur inside the wheat grains, only the adults are likely to be affected by the presence of *Ptinus tectus*, which seldom enters
grains. Experiments demonstrated that the rate of oviposition of a female *Sitophilus granarius* was reduced by the presence of an adult *Ptinus tectus* to an extent similar to that caused by the presence of a male *Sitophilus granarius* (Coombs & Woodroffe, unpublished). However, relatively few *Ptinus tectus* were present during the period of the experiment dominated by *Sitophilus granarius*, so this effect can have had little influence on the *Sitophilus* population.

(3) Incorporation of effects of change in nature of the food

As the experiment progressed, the *S. granarius* converted the original wheat into husk (hollowed-out grains) and frass (a powder consisting mostly of faeces). Since the number of adult *S. granarius* at any time depends upon both the rate of production of adults and their longevity, it is important to consider the effect upon longevity of this conversion, which must reach a maximum during the final population peak. The point has been investigated experimentally (Coombs & Woodroffe 1964). Longevity on husk was about half and on frass about one-sixth of that on wheat. If the longevity assumed for the peak period is reduced to one-half or one-quarter when performing the calculations, curves C₁ and C₂ of Fig. 5 are obtained. The result of this adjustment is that the peak of numbers and the time of extinction approximate more closely to those observed.

**MODIFICATIONS OF BASIC DATA AFFECTING NUMBERS OF **

**PTINUS TECTUS**

(1) Incorporation of effects of metabolic heating

As *P. tectus* is found most frequently in the superficial layers of stored food and as it would be likely to retreat from zones of high temperature, it could be argued that it is
unnecessary to apply increases in temperature of the wheat, due to the activity of *Sitophilus granarius*, to this species. Nevertheless, it was decided to use the amended temperatures because the grain formed a layer only 8 cm deep and the average ambient temperatures at the time of maximum heating were falling from about 16° C, and the heating would make conditions more favourable for *Ptinus tectus*.

The correction, applied during the period week 80 to week 110, increased the discrepancy between the observed and the calculated curves thereafter (Fig. 6, A).

(2) Incorporation of effects of interspecific interactions

The earliest major discrepancy between the calculated and observed curves for *P. tectus* arises at about week 110 when the calculated numbers far exceed the observed. This coincides with the peak numbers of *Sitophilus*. It was at this time that condensation, by providing drinking water, would have been expected to enhance the oviposition rate of the *Ptinus tectus* females. On the other hand, it is known that *Sitophilus* adults cause heavy mortality among eggs (Coombs & Woodroffe 1962), larvae (Coombs & Woodroffe 1970) and pupae (Coombs & Woodroffe 1963b) of *Ptinus tectus* and also lower its oviposition rate (Coombs & Woodroffe 1965). For these reasons, various levels of mortality were introduced into the calculations until a curve was obtained which approximated to the observed curves. Thus, in Fig. 6, curve B was obtained when a mortality of 70% was imposed for one generation from week 74; curve C represents a mortality of 90% of eggs laid by these adults; and curves D and E are the result of a return to 20% mortality by the next two generations. The calculations were simplified by being split into slightly overlapping generations. Thus, by imposing arbitrary but realistic mortality at the appropriate time good agreement between the calculated and observed curves was achieved but when, as the *Sitophilus granarius* population declined, mortality was allowed to return to normal, the recovery of the calculated values fell far short of the observed numbers (the average height of curve E in Fig. 6 is much lower than the lower of the two experimental curves).

(3) Incorporation of effects of change in nature of the food

The conversion of wheat into husk and frass by *S. granarius* has a direct (nutritive) and an indirect (physical) effect upon the *Ptinus tectus* population (Coombs & Woodroffe 1962, 1963b, 1965, 1970). Female *P. tectus* lay more eggs on frass than on husk or wheat, and larval development on frass is more rapid than on wheat. Also fewer eggs and larvae are killed by *Sitophilus* and *Ptinus* adults on frass and husk than on wheat. When we compared the oviposition rate on the three foods, cracked wheat instead of whole wheat was used in the experiments. This was done to avoid the high adult mortality which occurs on whole wheat and, since some cracked grains would have been present in the experimental wheat, to ensure that any differences demonstrated would be relevant to the most favourable part of the environment. Using this method, more eggs were laid on frass than on broken wheat but the difference was not significant statistically. Most of the eggs laid in the cracked wheat were found in cracks so it seems likely that, had uncracked wheat been used, a significant difference would have been demonstrated.

In order to take into account the changes in the food, the population curves were re-calculated once more, using the rate of development on frass as from week 108. The imposed mortalities of 70% and 90% were applied as in computing Fig. 6 (B and C) but the increased protection afforded to eggs and larvae (with a possible increase in oviposition rate) by the accumulation of frass and husk was regarded as reducing subsequent
Ecological succession in stored wheat

mortality from 20% to zero. The resultant curve (A in Fig. 7) shows a better agreement with the experimental curve but possibly rises too high at about week 180. The agreement is improved further by imposing 95% instead of 90% mortality at the relevant time (curve B, Fig. 7).

Thus by combining effects known to be possible from our experimental results on oviposition, developmental rates, mortality and species interactions, and introducing realistic trial values at appropriate times, it is possible to calculate curves of population change that correspond substantially with those representing our observed experimental populations.

**FINAL DECLINE OF THE *PTINUS TECTUS* POPULATION**

In the course of the succession experiment the population of *P. tectus*, which increased steadily following the extinction of *Sitophilus granarius*, reached its peak at about week 200 and then declined to extinction at about week 350. This decline has not been studied by means of analytical experiments and our simulation exercise does not cover it but one or two of the factors involved can be indicated.

In any closed system, consisting of a limited amount of a utilizable resource, exploitation of that resource over a period of time must result in a declining energy level in the system and the eventual extinction of the exploiting organisms. This declining energy level is illustrated in a general way by the successively lower peak numbers of the three species involved in the experiment as they became successively dominant. The decline of the *Ptinus tectus* population can be seen as part of this process but it seems likely that it was accelerated by additional factors. We have already described results (Coombs & Woodroffe 1965, 1970) which suggest that intraspecific density affects the quality (as opposed to the energy content) of the food, especially as regards specific essential components and, perhaps most important of all, homotypic conditioning could have contributed to the final decline.
DISCUSSION

When we described the population changes which occurred in two small bulks of wheat (Coombs & Woodroffe 1963a), we pointed out that it was unlikely that the successive species dominance could be explained directly from the results of single species laboratory experiments. It seemed probable that the explanation would prove to be complex, determined by interactions between species and the influence of the species on their environment. We have since performed a series of experiments (Coombs & Woodroffe 1962, 1963b, 1964, 1965, 1970) to investigate these possibilities and we discuss below how the interactions studied in these experiments might determine the numbers of each species present at any time.

At the start of the experiment the condition of the food favoured *Sitophilus granarius* in comparison with *Ptinus tectus*, while the latter also suffered from lack of drinking water. The temperature during the first summer conferred no particular advantage on either species but winter temperatures, although never lethal, were more detrimental to *Sitophilus granarius* than to *Ptinus tectus*. The rise in temperature induced by the very dense population of *Sitophilus granarius* later in the experiment was to the advantage of that species rather than *Ptinus tectus*.

The developmental stages of *Sitophilus granarius* were virtually free from adverse interactions except for intraspecific crowding. Adult *S. granarius* were susceptible to some crowding from *Ptinus tectus* adults, affecting oviposition; this was roughly equivalent to crowding by an equal number of *Sitophilus granarius* males. However, by the time that *Ptinus tectus* became sufficiently abundant to have a significant effect, the numbers of *Sitophilus granarius* were so large in proportion that it is doubtful if this inhibition was of any importance. In fact, at this stage, it is unlikely that any factor reducing oviposition would have any noteworthy effect, unless it caused a virtual cessation of egg-laying, because of the greatly reduced number of whole grains available for oviposition and development. The final decline of the *S. granarius* population was caused by lack of such grains, hastened by the reduced longevity of adults on husk and frass. At no time were the numbers of *S. granarius* likely to be influenced by the presence of *Ptinus tectus*.

Direct and indirect effects of *Sitophilus granarius* upon the growth of the *Ptinus tectus* population were, on the other hand, considerable. Those demonstrated in previous publications are brought together in Fig. 8. Here the changes in the *P. tectus* adult population during the experiment are illustrated in an arbitrary manner by the curved line. The level of the population at any point on the curve is determined by the relative strength of the factors opposing increase in relation to those encouraging increase. Thus, early in the experiment there were powerful forces opposing increase at a time when the forces tending to encourage it were weak. Later in the experiment the changes in the environment weakened the adverse factors whilst strengthening the ability of *P. tectus* to increase. Finally, towards the end of the experiment intraspecific factors opposing *P. tectus* increased in strength, food became poorer in quality and quantity and the population declined.

Perhaps the most noteworthy feature of the influence of *Sitophilus granarius* on *Ptinus tectus* is the multiplicity of its effects. Initially, by increasing mortality and reducing oviposition and development, it acts as a powerful depressant on the *P. tectus* population. At the same time it changes the nature of the food and provides protective refuges for the *P. tectus* larvae, so that its depressant effect declines. The change in the food is advantageous to *P. tectus* but detrimental to itself and hastens its own extinction. When it
Factors affecting the numbers of adult *Ptinus tectus*

*S. granarius* changes WHEAT --- into --- FRASS and Husk --- as population of *P. tectus* increases intraspecific effects operate more strongly and the environment becomes conditioned.

Fewer eggs killed with result that on fewer eggs oviposition rate less retarded.

Development retarded with result that on adult weevil larval mortality reduced.

Development speeded with result that on mortality reduced.

Egg potential fecundity increased with result that on eggs protected in frass reduced.

Crowding reduced with result that on mortality reduced.

Direct food effect with result that on interspecific effects.

**Fig. 8.** Summary of the interactions likely to affect the numbers of *Ptinus tectus* in the presence of *Sitophilus granarius* when the food supply is not renewed. (Broken lines in the body of the diagram represent interactions indicated experimentally but not statistically established.)
finally dies out the texture and nutritive value of the food is more suitable for *P. tectus* than the original wheat would have been if ground into flour. For this reason, following its extinction, the rate of increase of *P. tectus* not only recovers but is enhanced.

All of the factors shown in Fig. 8 have been demonstrated experimentally. The calculations described above show that a rough approximation to the observed population changes of *Sitophilus granarius* can be made using published values for the intrinsic rate of natural increase. Much better approximations are possible, especially for *Ptinus tectus*, if the available experimental data are used to make weekly, step-by-step estimates of population size. These estimates are further improved if adjustments are made whenever interactions between the species, either direct or indirect through the effects of temperature or food change, are likely to alter the developmental rate, mortality, longevity or fecundity of either species. An excellent fit to the observations can be obtained by allocating to these specific factors values that are reasonable interpretations of the interaction experiments. We would suggest from this that not only do the interactions occur but they influence the numbers of *P. tectus* significantly. If one considers the two factors affecting *P. tectus* here—natality (or mortality) and speed of development—the more important in achieving approximation is natality. This, although seemingly contradicting what would appear logical from a study of formulae for increase (i.e. that changes due to developmental period will vary directly but changes in natality and longevity only as the logarithm) is a function of the limited number of generations involved and the restricted and variable environment.

As has been emphasized throughout this paper, the explanation of the population changes illustrated by the diagram has involved making a number of assumptions. The environmental changes which occurred in the course of the experiment were gradual and progressive. The breakdown products of wheat—husk and frass—accumulated simultaneously, mixed together and mixed also with intact grain and dead insects. The effects of these substrates were investigated individually, but not in mixtures of varying composition. For example, we have shown that frass, on its own, protects the developmental stages of *P. tectus* from the various adverse effects of the presence of *Sitophilus granarius* and *Ptinus tectus*. It also minimizes these effects by shortening the adult life of *Sitophilus granarius* and by stimulating rapid development of *P. tectus* larvae. From the fact that *P. tectus* prefers to oviposit in frass, we suggest that these effects were operative, to some extent, under the conditions of the experiment, when the various substrates were mixed together, but we have no proof that this was so. Similarly, in our calculations based upon the experimental results, new values were introduced abruptly, whereas they would have become operative gradually in the actual experiment.

The numbers of adults present at any one time reflects a combination of the productivity of the species and the longevity of the adults. As *P. tectus* adults, in the absence of drink, live for only a short time compared with *Sitophilus granarius* adults, the relative productivity of *Ptinus tectus* compared with *Sitophilus granarius* is correspondingly underestimated in our graphs, which use adult numbers as indicators of population growth. The order of difference between the population levels when both species are present renders this underestimate unimportant. However, our argument centres round changes in the level of the *Ptinus tectus* population, so a change in the length of adult life during the experiment will be of importance. We have already mentioned the shortening of adult life of *Sitophilus granarius* on frass and husk and have demonstrated that this lowers the calculated population level and hastens extinction. In the case of *Ptinus tectus*, the most important factor affecting longevity which changed during the experiment was
the availability of drinking water. This was present, in the form of condensation, at the peak of the *Sitophilus* population and, by lengthening adult life, may have given rise to a spurious increase in observed numbers. In fact, at this time, *S. granarius* was exerting a strong depressant effect upon the numbers of adult *Ptinus tectus* and the observed population level declined. The only possible result, therefore, will have been some underestimation of this depressant effect.

The succession experiment was carried out in closed tanks but was based upon observations on the fauna of birds' nests (Woodroffe 1953) and a study of an empty granary (Coombs & Freeman 1955). In the latter a change in dominance was found from *Sitophilus granarius* in food residues of high quality to *Ptinus tectus* in residues of poorer quality and finally *Attagenus pellio* in residues of poorest quality. Hunter (1965) examined the fauna of a derelict flour mill over a period of 5 years and he reported a similar succession of *Sitophilus granarius* followed by *Ptinus tectus* and finally *Attagenus pellio*. Experimentally, Coombs & Woodroffe (1968) studied an infested bulk of wheat in which emigration and immigration were possible. This situation was more complicated than the experiment in closed tanks and more species were involved. The results were not directly comparable but the processes at work appeared to be similar.

It would seem, therefore, that the imposition of a closed system, preventing entry and egress, had no significant effect upon the course of the succession, although it probably affected the rate of change and possibly the severity of the interactions.

A point of some practical importance concerning food storage arises from the results of rearing *Ptinus tectus* on conditioned foods (husk and frass) (Coombs & Woodroffe 1965). These experiments indicated that adults reared on these foods had a higher potential fecundity than adults reared on unconditioned foods but that this potential was only realized when oviposition occurred on unconditioned foods. This situation is particularly applicable to the grain residues which accumulate beneath floorboards, in wall cavities and in other inaccessible places in storage buildings. Such residues often remain undisturbed for long periods of time, support a varied fauna of storage insects and show the sort of successional changes, associated with deteriorating food quality, which our experiment demonstrated. The fauna of such residues would, if the results mentioned above were generally applicable, have an enhanced fecundity when infesting clean stocks of stored foodstuffs.

The overall results of the series of investigations discussed in this paper have relevance to certain general problems of pest control. The replacement of broad-spectrum insecticide by compounds with more selective action has created new problems in this field. Hall (1969) gives a graph illustrating the changes in pest importance in bagged maize stored in Africa in relation to insecticide use. Initial heavy infestations of weevil (*Sitophilus* spp.), *Tribolium* and mites were markedly reduced in the early 1950s due to the use of lindane. At this time there was an increase in moth infestation. In the early 1960s, following the use of malathion, there was a further fall in weevil, *Tribolium* and mite populations to a very low level, while moth infestations became heavy.

One obvious explanation of this phenomenon is that the insecticide, in addition to controlling the beetles, eliminates the parasites of the moths, thus releasing them from a degree of natural control. However, Graham (1970), studying the infestation of maize in Kenya by *Sitophilus zeamais* Mots., *Tribolium castaneum* (Herbst) and *Ephestia cautella* (Walk.), came to the conclusion that parasites played little part in controlling moth numbers. He found that a predatory mite which attacked the eggs was probably the most important factor. We suggest that, in this type of situation, interactions between the
pest species themselves, of the type we have described, may help to explain an outbreak of moth following elimination of a dominant beetle pest by a selective insecticide. We have already described one instance which could be explained in this way (Coombs & Woodroffe 1968). A bulk of wheat, stored in an unheated building in southern England, was infested experimentally with several grain pests. A moth, Hofmannophila pseudospretella (Staint.), remained at a relatively low level until the dominant beetles (Sitophilus granarius and Oryzaephilus surinamensis (L.) ) began to decline. It then increased to become the dominant species, just as Ptinus tectus did in the earlier succession experiments (Coombs & Woodroffe 1963a). We suspect that interspecific interactions were at least partly responsible.

As a final point we would emphasize the general ecological significance of our findings. It is clearly important to know that two species of markedly different habits and requirements, which would not be expected to compete with one another to any significant extent, nevertheless interact to a considerable degree and in many different ways in a very simple and homogeneous environment.

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SUMMARY

(1) In an unrenewed, closed environment of wheat grains there is a succession of dominant insects, firstly the grain weevil, Sitophilus granarius (L.), secondly the Australian spider beetle, Ptinus tectus Boield., and finally the fur beetle, Attagenus pellio (L.).

(2) A comparison is made between the numbers of Sitophilus granarius and Ptinus tectus observed experimentally with the numbers to be expected if these species are bred separately, but otherwise in the conditions of the experiment.

(3) The calculated values for Sitophilus granarius, when amended to account for metabolic heating and a shortened adult life on frass and husk, agree closely with those observed. The calculations for Ptinus tectus diverged widely from those observed during and after the maximum numbers of Sitophilus granarius.

(4) Arbitrary but realistic modifications to the basic data used in the calculations, as suggested by known interactions between the two species, enable a close approximation of the two curves to be achieved. This is taken to show that the interactions play an important rôle in determining the numbers of Ptinus tectus and a diagram is provided to illustrate all the known interactions.

(5) The complicated rôle of Sitophilus granarius in what is basically a very simple ecosystem and the implications for pest control are discussed.

REFERENCES
Ecological succession in stored wheat


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