STRUGGLE FOR EXISTENCE
THE *TRIBOLIUM* MODEL: BIOLOGICAL AND STATISTICAL ASPECTS

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> "... *When we mean to build,*
> *We first survey the plot, then draw the model;*
> *And when we see the figure of the house,*
> *Then must we rate the cost of the erection,*"
> *King Henry* IV (Part II), Act I, scene 3

CONTENTS

GENERAL INTRODUCTION

The purpose of this paper is to present an account of a three-year cooperation between the Hull Zoological Laboratory of The University of Chicago on the one hand; the Statistical Laboratory, University of California, on the other. The objective of this cooperation is to make an initial contribution towards understanding

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The experimental work mentioned in this paper has been supported jointly by grants from The Rockefeller Foundation and the Dr. Wallace C., and Clara A. Abbott Memorial Fund of The University of Chicago. Thomas Park expresses his deep appreciation to the following friends for criticism, constructive suggestions, and advice: Thomas Burnett, Charles Elton F.R.S., A. E. Emerson, P. W. Frank, Don W. Hayne, David Kendall, P. H. Leslie, M. B. Lloyd, and K. E. F. Watt.

The statistical part of this paper, done at the Statistical Laboratory, University of California was done with the support of the Office of Ordnance Research, U. S. Army under Contract DA-04-200-ORD-171.

some of the complicated ecological phenomena frequently referred to in general terms as "struggle for existence." Specifically, we shall be concerned with the "competition" that exists between two species of flour beetles (*Tribolium*) when reared in the laboratory under selected experimental conditions. Our intent at this time is not so much to reach definitive conclusions but, rather, to establish a broad pattern from which later work can take its departure.

In any cooperation of a group of biologists and a group of statisticians there must be phases for which only one of the two groups is responsible. However, there is also an important phase in which the responsibility is shared. The latter is concerned with establishing a bridge between the various elements of statistical theory of the given phenomena and the phenomena themselves. In consequence, this paper is divided into two parts. Part I summarizes broadly the biological aspects conducted at The University of Chicago. Part II summarizes two other phases of the work, the purely statistical phase, performed at the Statistical Laboratory, and this includes the results of C. L. Chiang, Lucien Le Cam and Bernard Sherman, and the cooperative phases.

PART I. BIOLOGICAL ASPECTS

1. Introduction

The focal objective of population ecology is the understanding of those processes responsible for census-trends of species-populations living in natural habitats. Owing to the inherent complexity of the processes this is an objective far easier to state than to fulfill. Superimposed on this is another complication. The environment is characteristically variable and varying. The population responds slightly, or markedly, to this variation and, in so doing, may modify in turn its environment. Such variation is not under the control of the investigator although he may systematically record it by initiating in the field a sustained program of census, and environmental measurement—a program leading to an impressive accumulation of physical and biotic information. But the information is likely to be difficult to analyze and even more difficult to generalize conceptually. Despite such handicaps, however, this approach must remain the central one in the study of natural populations for the self-evident reason that it, of all others, *directly* comes to grip with conditions and responses as they occur in nature. No implication is intended that the direct approach lacks power; or indeed that its power cannot be increased. More judicious collection of relevant data, greater utilization of multivariate analysis, and in some cases, actual experimentation in the field, are valuable extensions that must find further perfection and adoption.

The difficulties that arise when populations are studied by direct mensuration in the field, however, have led various investigators, for various reasons, to several sorts of substitutes. Even though differing markedly in conception such substitutes can be characterized as "models" and share in common the features (1) that they are presumed to depict the workings of at least a part of nature but (2) in a guise purposely designed to enhance the interaction of certain factors, diminish (control) other interactions, and eliminate still others. Such models are either *mathematical* or *laboratory-experimental* and in some instances the two have been used in conjunction.

The mathematical models can be *deterministic* or *indeterministic*.[1] The former make no allowances for chance variation while in the latter this is introduced as an integral component of the system; for example, population size may be treated as a random variable [1]. Deterministic models are important historically in the sense that they have provided stimulus for both abstract and experimental work and, in addition, have imposed a necessity to think about problems in terms of the *concepts* involved [2]. These models are largely concerned with *interspecies* relations; especially those cases where two species compete for the same resource and where one species feeds upon another. Whether rightly or wrongly, the two-species models seem to be enjoying less reception among ecologists owing in part to the oversimplification of their underlying assumptions; see Ullyett [3] for a critical statement of this position. The "logistic curve" (a deterministic equation of single-species increase) has been retained by some at least, not because of an inherent interpretative value, but simply because it affords a convenient way of describing population growth which, for some reason, is so often symmetrically sigmoid. Classical papers on ecological events from the viewpoint of mathematical determinism are those of Verhulst [4], Ross [5], [6], Pearl and Reed [7], Lotka [8], [9], [10], and Volterra [11], [12]. Summaries in book form are to be found in Kostitzin [13] and D'Ancona [14].

To date, the impetus derived by ecology from *indeterministic* models has been negligible. Probably this reflects the fact that these models are more difficult to erect, to understand, and to apply. But to us at least, they are more satisfying intuitively than their deterministic counterparts. Ecological events *are* variable and subject to chance modification. Also, as later we shall show, they have both the potentiality and actuality of proceeding to more than one conclusion and a model which incorporates a mechanism permitting this to occur, seems to hold considerable promise. Whether such models will ever become rewarding for population ecology (as they have for evolutionary genetics) is quite debatable. But it does seem that they deserve a hearing—especially if the theoretical statistician and the empiricist can be persuaded to collaborate in a serious and sustained way. Papers on probabilistic (stochastic) theory, relevant in terms of the present emphasis, include the following: Yule [15], Feller [16], Kendall [17], [18], Arley, [19], Neyman [20], Fix and Neyman [21], Bates and Neyman [22], and Chiang [1].

The approach through the laboratory, like that through mathematics, also involves models. The two approaches are similar in that both are abstractions of nature designed to illumine natural phenomena but they differ in that the results of work in the laboratory obviously take empirical form—nature is modeled by derived data rather than by formulas.

Laboratory models have dealt with the same "struggle for existence" phenomena that have occupied the mathematicians, namely: population growth, components of intraspecies competition, interspecies and intergenus competition, predator-prey interactions, and host-parasite interactions. Some of this research has been con-

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[1] There is another mathematical approach, very common in quantitative biology, which does not involve the use of models but which has application for population ecology. Neyman refers to this as "interpolatory procedure"—a particular kind of mathematical treatment of phenomena by which a flexible formula is invented to fit the data. Interpolatory procedure makes no attempt to guess at the *mechanism* underlying the phenomenon. To use an example from genetics, it is the approach of Galton and Karl Pearson in contradistinction to the approach which grew out of Mendel's observations and which led to a "structural model."

ducted with prior reference to deterministic models and some has avoided this association. This is illustrated in the accompanying tabulation in which selected publications falling under both approaches are listed:

I. *Laboratory research utilizing deterministic models:*
  (1) Pearl [23]: logistic growth of *Drosophila* populations.
  (2) Stanley [24]: mathematical theory of growth of *Tribolium* populations.
  (3) Gause [25]: competition, and predator-prey interactions, among *Protista.*
  (4) DeBach and Smith [26]: host-parasite interactions in insects.
  (5) Crombie [27], [28]: intergenus competition in insects.
  (6) Fujita and Utida [29]: population density and rate of growth of insect populations.
  (7) Strawbridge [30]: intraspecies competition among and between stages in *Tribolium* populations.
  (8) Rich [31]: cannibalism, fecundity, and intraspecies competition in *Tribolium.*
  (9) Watt [32]: an experimental approach to the problem of the optimal yield.

II. *Laboratory research not utilizing mathematical models:*
  (1) Pearl [33]: fecundity and crowding in *Drosophila.*
  (2) Park and Woollcott [34]: fecundity and conditioning in *Tribolium.*
  (3) Allee, Finkel, and Hoskins [35]: growth-promotion and conditioning in fish populations.
  (4) Utida [36]: population density and progeny survival in weevils.
  (5) Park [37], [38]: interspecies competition in *Tribolium.*
  (6) Burnett [39]: host-parasite interactions in insects.
  (7) Frank [40]: intergenus competition in cladocerans.
  (8) Birch [41]: interspecies competition in grain beetles.
  (9) Sokoloff [42]: interspecies competition in *Drosophila.*

In the remarks shortly to follow we wish to illustrate models by reference to problems, and phenomena, derived from studies of flour beetles (*Tribolium*). The intent is neither a systematic nor a historical review of literature. That would be too long and quite pointless for present purposes. Rather, the intent is twofold: (1) to illustrate selected features of laboratory models of this type and (2) to provide a background for the later statistical discussion in which it is suggested that the "*Tribolium* model" (itself a laboratory-biological model of nature) in turn, and in some of its simpler aspects, can be modeled mathematically by *probabilistic* treatment. In this way we hope not only to contribute something which is in harmony with the tradition of these Symposia but, also, to show that these sorts of models, reflecting the interests of three investigators, can be studied advantageously as part of a common problem.

Suppose we ask this question: what technical and biological attributes should be possessed by a laboratory-experimental model that is adjudged as excellently adapted for study of population phenomena? An answer to the question appears as a list of specifications.

(1) *Census.* It should be feasible to take a complete count of the population including all component stages. The disturbance brought about by the census should be negligible in terms of survival and the labor involved should not be prohibitive.

(2) *Generation time.* The interval from one generation to the next should be short enough to permit definitive results to be obtained within a realistic span of time.

(3) *Age and sex distributions.* It should be possible to diagnose the age and sex of the populations' membership so that age and sex distributions can be constructed.

(4) *Replication.* It should be always possible to replicate any design in numbers sufficient not only to facilitate adequate statistical treatment of data but, also, to allow empirical study of the distribution of outcomes of experiments.

(5) *Physical environment.* It should be possible to control, and/or to manipulate by plan,
  (a) factors of the physical environment external to the cultures that are deemed to have probable ecological importance (for example, temperature, moisture, light), and,
  (b) the size of the physical habitat available to the population and its surface-volume configuration (for example, weight, volume, dimensions; of space or medium).

(6) *Trophic environment.* It should be possible to control the quantity and quality of the food supply within reasonable limits, or barring that, to measure how the food changes as it is used.

(7) *Stock cultures.* It should be possible to maintain stocks of the experimental organism with a minimum of attention.

(8) *Observation of behavior.* It should be possible, in populations of various densities, to observe all stages of the species in order to evaluate the role of behavior in affecting (or not affecting) a particular response.

(9) *Genetic situation.* It should be possible to develop and maintain stocks constituted genetically as required by the particular problem. The species should lend itself to desired schedules of inbreeding and outcrossing.

(10) *Combination of models.* Potentiality for further study is impressively increased if two or more one-species models can be combined successfully into a single structure which simulates some sort of ecologically realistic *inter*-species relation.

From this list a definition of a laboratory-experimental model might be strung together in the following way. A population exhibiting a relatively rapid life cycle in a not too artificial laboratory habitat; cultured under easily controlled, yet manipulatory, environmental and trophic conditions; for which repeated censuses of all stages can be taken with negligible disturbance, and for which adequate replication is feasible.

Laboratory models of population phenomena are sometimes criticized as being "artificial." If by this is meant that findings derived from such studies cannot be applied directly to outdoor ecology, then the criticism has a type of validity. If, however, "artificial" is intended to imply triviality, then the criticism is unfounded. The characteristics of *natural* populations are understood less well than those of their laboratory counterparts and progress in this area is apt to be slow and difficult. Our point is that laboratory and deductive-statistical efforts can accelerate the understanding of *all* populations. This acceleration may be realized (1) by selecting, but circumscribing, problems adapted from nature; (2) by analysis of such problems, this to be followed by rephrasing the problem for further analysis; (3) by moving, conceptually and technically, from field to laboratory to field, and (4) by attempting to obtain data from laboratory and statistical studies in a form more suitable for application in the field. In different words, a certain sort of artificial quality in the laboratory model can be just the feature that favors progress. Elsewhere (Park [43]), this was put another way: "The laboratory models, though not simple, are simplified; they are under a regimen of planned control, and their intrinsic interactions are likely to be intensified. To this extent they are unrealistic. But they remain, nonetheless, quantitative *biological* models and their unrealistic aspects may be a virtue instead of a vice. This is to say, they can contribute to the maturation of ecology, at least until that time when they are no longer needed."

There is another face to the coin. This, less apologetic and more positive, can be put as follows. To date, have studies in the laboratory actually contributed anything of value for the field worker? Not being experienced enough to answer this at first hand we consulted several persons who are. The following interesting answer was received from Dr. Thomas Burnett of the Canadian Department of Agriculture and is quoted with his kind permission: "(a) Laboratory models are erected to answer questions encountered in years of field experience. (b) Many field programs are designed on the basis of results obtained in the laboratory. (c) After a preliminary survey, which may last for many years, field research workers reach a point where they turn to laboratory models. A field problem often becomes a study of the mechanism operating in a natural community and, to date, laboratory populations have offered the best means of analyzing these mechanisms."

2. Attributes of the Tribolium model

Let us now examine the attributes enumerated above as they pertain specifically to the *Tribolium* model. To do this it is necessary to introduce a few points about the beetles and their husbandry.

The genus *Tribolium* is constituted by 26 different species (Hinton [44]). Two of these have demonstrated their suitability for population research and have received more than a little study. The two, *Tribolium confusum* and *Tribolium castaneum*, spend their entire life-span, and that of successive generations, in finely-milled flour. This fact has several adaptive implications in terms of the model. It means first that infested flour can be sieved in order to recover beetles of all stages for purposes of counting (point 1). This counting can be quite accurate and we have no evidence so far that the procedure is deleterious. Since flour is exclusively the food supply, and, since the beetles live only in it and on its surface, it means that flour is at one and the same time the physical milieu and the trophic environment. Because flour can be weighed; because it assumes the configuration of its container; because it acquires the temperature and moisture characteristic of its external climate; and because its nutritive quality can be reasonably well standardized, it follows that the attributes listed as points 5 and 6 (physical environment and trophic environment) are realized rather well by the *Tribolium* model. There is another favorable aspect. Even though they are found in other places, *T. confusum* and *T. castaneum* occur with highest incidence over much of the world in cereals milled by man. It is likely that these two species were either preadapted to flour or that they are now in process of becoming adapted to this medium in the evolutionary sense. It is amusing to note that they are reported (Andres [45]), from a Pharaonic tomb (about 2500 B.C.) at which time, presumably, they utilized flour. The inference from these points coupled with the fact that flour is eminently satisfactory as a total habitat, suggests that the *Tribolium* model is more "natural" than might appear at first glance. Regarding the genetic situation (point 9) it can only be said that thus far stocks have been produced as required but much more needs to be done along this line. The final, and a major, feature is that by combining the two species into one interacting population a model of competition is thereby created (point 10) which possesses favorable technical and conceptual qualifications.

However, there are also drawbacks to *Tribolium.* Procedures involved in censusing, though not "prohibitive," are disagreeably prolix. The length of a generation (roughly a month from egg to egg at 29°) means that several years or more are often required to obtain definitive findings for many sorts of population problems. Replication can be, indeed must be, adequate but an experiment of broad scope can be conducted only with the aid of sufficient manpower. It is essentially impossible to observe the beetles' behavior *in* flour—a decided handicap in understanding certain phenomena. The beetles are prone to several sorts of ectoparasitic and endoparasitic attacks. This can be turned into an interesting advantage (Park [37]), but ordinarily the elimination and sustained control of these invaders is a tiresome bore. Adult beetles cannot be quickly sexed and, more importantly, they cannot be diagnosed as to age. It has been impossible, therefore, to construct accurate age-and-sex distributions for various sorts of populations. Lastly, in the two-species model of competition, the immature stages (eggs, larvae, pupae) are not differentiable as to species, the consequence being that the data derived from this model are based on adult numbers only.

Thus, though *Tribolium* is far from ideal, it does offer distinct advantages and, from a prejudiced point of view at least, appears to have as great a combination of attributes favorable for ecological population study as any species yet used in the laboratory analysis of such problems.

3. Empirical aspects

In this section we wish to ask, and attempt to answer, the following three questions:

(1) What are the known physical and biological components of the *Tribolium* model? (*Components.*)

(2) What approaches are available when populations are studied in the laboratory? (*Laboratory approaches to population study.*)

(3) Can both deterministic and indeterministic phenomena be illustrated empirically by population studies of *Tribolium* species? (*An empirical population experiment.*)

These questions will be considered one-by-one and then the purely statistical aspects will find discussion in the section that follows.

(i) *Components.* It is convenient to discuss the components of the *Tribolium* model by reference to figure 1 in which an attempt has been made to organize and relate these elements in a reasonably realistic (though not comprehensive) fashion. The figure makes use of the terms "habitat," "processes," "survival responses," and "pathways." *Habitat* refers to the physical environment occupied and exploited by the beetles. *Processes* are those organismic activities known, or suspected, to affect numbers through their single or joint influence on responses. *Responses* are the natality and mortality attributes which, through interrelation, bring about control of population numbers. The habitat can influence a process (and sometimes the reverse) and a process can influence a response. Such channels are *pathways.*

The *habitat* falls into two categories. There is the physical environment imposed by design and that imposed by the beetles' collective activity. The former is under the initial control of the investigator; the latter, not. In much of the work done at Chicago a "standard microcosm" has been used which consists of a glass vial (9.5 × 2.5 cm.) into which eight grams of homogeneous medium is introduced. This defines the habitat nutritionally and spatially. When the vial acclimatizes in a dark incubator at constant temperature and humidity, the flour assumes the incubator's characteristics and through this the habitat finds climatic definition. However, the beetles modify the habitat in some way proportional to the size of their population and to the length of time the flour is occupied. The medium can be reduced in nutritive quality, in particle size, and in volume; it can accumulate excretory waste-products ("conditioning"); and it is probable that it may change in temperature and moisture ("microclimate"). Whether such modifications are effective in altering responses is a matter always to be kept in mind but one not predictable without direct study.

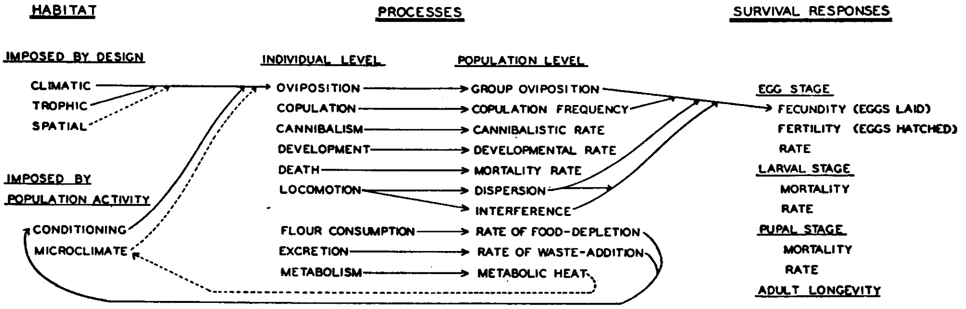


FIGURE 1

Major components of the *Tribolium* model. See discussion in text.

The *processes* are of biological origin and become ecologically relevant if it is demonstrated that they influence a response. This is to say, a beetle's physiological or behavioristic activity has meaning only when that activity directly or indirectly affects natality and/or mortality. Figure 1 specifies an array of processes characteristic of individual organisms, this then being translated in the next column to the form assumed in characterizing the population. Thus, single *Tribolium* may lay eggs (oviposit), copulate, eat eggs and pupae, develop, die (or live), move, eat flour, and modify flour through liberation of metabolic wastes and heat. At the group level, however, such items assume statistical form, namely: group oviposition; copulation frequency; rate of cannibalism, development, and mortality; dispersion patterns; "interference," and rate of food depletion and habitat contamination. The naming of an attribute for an individual means merely that the attribute is known to exist and have group significance. Naming it for the population connotes the intensity of that attribute.

Brief reflection will show that these activities are related to the population density of the beetles present ("density-related phenomena"). One fecundated female in eight grams of medium under defined conditions would lay eggs at her own inherent rate. But the group oviposition of, say, 100 females considered as members of a balanced population would be affected by dispersion, copulation frequency, quality of food, possible beetle contacts (interference); and so on. This rate would not be the simple summation of the individual productivity of each of the 100. Accordingly, any assessment of the component processes of the model must take into account the crowding and oviposition of the population itself.

The *responses* are considered separately by stages since each stage has a certain individuality in terms of its role in population behavior and since the census procedures permit us to concentrate on a particular stage if so desired. The life-cycle of *Tribolium* proceeds from egg, to larva, to pupa, to adult requiring for its completion approximately a month at a temperature of 29° C. The egg (in which embryogenesis occurs), and the pupa, neither feed nor move. The larva and adult are locomotory, take food, and, in addition, the latter is reproductive. As shown in figure 1 we are concerned with mortality of all stages; with rate of development of the three immature stages, and, for eggs, with number actually laid (fecundity). Stage-specific mortality is the mechanism by which a decrease in number is achieved; fecundity, measures the birth-rate and constitutes the mechanism of increase. Interrelation between mortality and natality determines "survival"; that is, what actually happens to the population. Rate of development from egg to reproducing adult describes an interval which may reflect the velocity at which changes in beetle numbers occur. Adult longevity partially expresses the duration of the reproductive period. Apart from immigration and emigration—elements obviously excluded when closed containers are used—all possible "responses" are accounted for in the above enumeration and in figure 1.

The *pathways* are to be viewed as avenues from cause to effect. But the avenues exist much more as a reticulum than as simple, direct highways. In addition, many such pathways are imperfectly understood; indeed, some are not understood at all. An attempt has been made in figure 1 to depict a partial set of pathways purely to illustrate this phase of the model.

We examine the response "fecundity" and ask what are certain of the pathways through which it is influenced. It is known that the climatic and trophic components of the habitat affect the egg-laying of single and grouped females. It is suspected that spatial relations of the habitat do likewise. Thus, all elements of the habitat imposed by design affect oviposition. Further, if through population processes (see arrows of figure 1) the physical features of the medium are additionally changed in nutritive and contaminative respects (conditioning), and, if (say) the temperature is consistently elevated with increase in population density (microclimate), then these modifications would be superimposed on the initial conditions. This could alter the process of oviposition, and group oviposition, and thereby the birth rate.

Examining the processes in more detail we draw an arrow in the figure from "group oviposition" to "fecundity response." The former specifies merely that a population of females lays eggs; the latter, the rate at which eggs are actually laid under defined conditions. Fecundity is influenced, however, by other processes as well as by the habitat. It is known that the incidence of meeting, and mating, of males with females ("copulation frequency") affects fecundity within certain limits (Park [46]). This then is introduced into the model.

Dispersion also claims our attention. In their movements, adult beetles establish a nonrandom dispersal within the vial of flour. For example, when a series of 16 "standard populations" was vertically censused in four strata from top to bottom the following average distribution of adult *T. confusum* was obtained (unpublished):

Stratum	Mean per cent of adults
Surface of medium	7
First third of medium	45
Second third of medium	26
Third third of medium	22

Dispersion patterns can merge with other processes in affecting fecundity by bringing the beetles into relation with possible vertical or horizontal stratifications of the habitat, by keeping a subsample of them on the surface of the flour where group-oviposition would undoubtedly be more difficult, and by "interference." With reference to the last process it is known for several organisms (notably *Drosophila melanogaster*, Pearl [33]) that jostling between population members reduces fecundity. In the fruit fly this seems to result from reduction in time available for oviposition, copulation, and feeding, and from general "overstimulation." *Tribolium* adults meet frequently in dense populations and such contacts may well constitute effective interference. On the flour-surface of a well-populated vial, for example, the mass of beetles is in highly agitated motion. To our knowledge there is no *direct* observation that interference reduces the beetles' fecundity. But there is indirect evidence from the reports of Boyce [47] and Rich [31] who showed under relatively optimal conditions that a loss in number of eggs hatched (fertility) with increase in crowding was more than could be accounted for purely on the basis of an egg being eaten by an adult. This suggests an interference-process based on number of contacts which is over and above the cumulative influence of habitat-factors, cannibalism, and other processes. Accordingly, it is reasonable to infer that interference has a reality, that it stems from locomotory movement leading to differential dispersion and contact, and, therefore, that it merits inclusion in the model.

From this discussion of the *Tribolium* model we have become aware of certain of its physical and biotic components and have suggested something of its inherent dynamics. The model is "simple" in two major respects: (1) certain components can be controlled as others are quantitatively studied and (2) the influence of other organisms is eliminated. However, the model still remains intricate as those of us who have struggled with it can attest. But it retains two virtues. It is truly a *biological* model which mimics natural events with considerable realism. And it gives promise of yielding more information about the organization of populations. Let us now turn to other aspects.

(ii) *Laboratory approaches to population study.* From the perspective of the laboratory investigator three approaches are available when population phenomena are to be studied. Each approach asks a different sort of question but the answers are interdependent and commonly bear on the larger problem under attack. There is reason to discuss the matter here because this will provide the necessary transition between the foregoing section on components of the *Tribolium* model and the empirical and statistical material shortly to follow. We identify the three approaches as "assay," "analytical," and "populational."

The approach through *assay* has as its objective the accumulation of general and basic knowledge when the experimental organism is not under realistic population conditions. In working with *Tribolium* we need information about all "processes," both at the individual and group level. Data are obviously required about life history, oviposition, and mortality in relation to selected habitat factors. The assay is useful not only in appraisal of what the beetles *do* in specific situations but also as a guide for the later construction of an experimental design into which population aspects are introduced. To illustrate an assay suppose we ask this question. What are the fecundity responses of *Tribolium confusum* and *T. castaneum* when all habitat factors are kept constant except temperature, when cannibalism is negligible, and when crowding does not exist? These questions have been answered (Park and Frank [48]) for three temperatures (24°, 29°, 34°) and the findings, expressed as mean number of eggs laid per female per 72 hours for 30 days, appear below:

Temperature	T. confusum	T. castaneum
24°............................	14.7 ± 0.27	19.1 ± 0.35
29°............................	38.2 ± 0.45	50.5 ± 0.70
34°............................	42.7 ± 0.56	57.2 ± 0.68

The tabulation shows for the condition of assay (1) that the temperatures are physiologically permissive for oviposition by both species; (2) that fecundity increases significantly with increase in temperature, and (3) that *T. castaneum* has a significantly greater rate of egg-laying than does *T. confusum.* It is obvious that data like these, concerned with important components of the model, constitute information essential for research extension. There is no point in further multiplying such examples.

It is more meaningful to discuss populational and analytical approaches together than separately. Simply put, a *populational* finding is a description of some group-phenomenon derived from census-data, the latter being obtained from the histories of a series of continuously breeding cultures. An *analytical* finding, on the other hand, is one which takes its *origin* from the same population data but identifies the temporal pathways that explain the observations. An attempt to clarify these distinctions in abstract form appears as figure 2 and, shortly, we return to the question by means of empirical illustrations.

Let us examine figure 2. Suppose we have demonstrated the result shown in the top diagram. There it is seen that the two species (solid and broken lines) have been reared together in a specific design (A) for a number of generations. We know from appropriate "controls" that *each* species survives successfully in the A-conditions when cultured only with itself. We therefore conclude that elimination of one species-population by the other is an expression of some cumulative superiority of the winner over the loser when the two share a common habitat. We label this phenomenon "interspecies competition" and assert that the fact of such competition has been proved and that its end-result is described. The position at this point is that the census observations have identified the phenomenon but have not explained its causation.

Having this knowledge the investigator is confronted by two choices relative to his later work—selections which in a sense are *conceptual* alternatives. The choices, of course, are analytical or populational. We state these two so dogmatically only to dramatize their difference. We recognize full well that they are not mutually exclusive since, clearly, one approach is catalyst for the other, and contrariwise. Our intent is to examine briefly what really amounts to the philosophy underlying further utilization of the model. If the investigator decides to work analytically, taking his departure from the original population finding, he states in effect: "I am most concerned with examining the *pathways* through which one species is eliminated in the presence of the other." This yields more and more information about the experimental material and the mechanism controlling the model. Or, the investigator may remark: "I have greater interest in examining the ramification and variability of the *phenomenon* when the model is subjected to new, though ecologically realistic, designs." This is apt to yield knowledge not so interpretative in respect to dynamics but more related to events that occur in outdoor ecology.

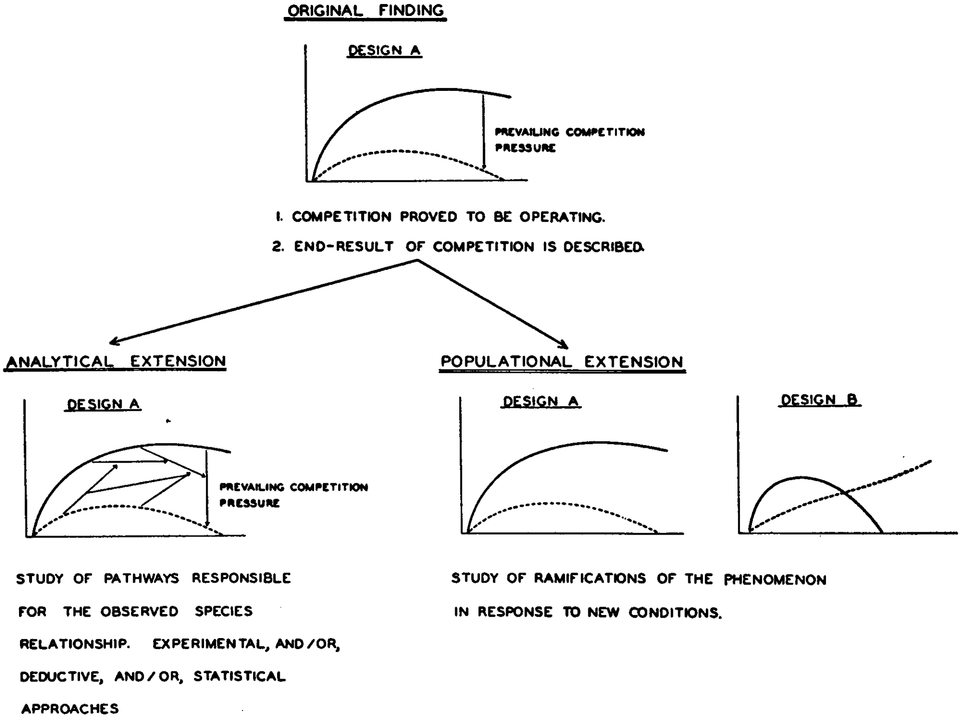


FIGURE 2

Schematized representation of methods of studying population problems. See discussion in text.

We return to figure 2. The left-hand arrow leads from the original finding to its analytical extension. Here, it must be assumed that the facts of competition earlier discovered for design A can be reaffirmed by repetition. Attention now centers on the pathways responsible for the result. If successful, the investigator is able to interpret the temporal changes in species numbers as functions of the dominant interactions. However, it is only fair to report that, to our knowledge, no fully satisfactory interpretation of this sort has yet been achieved. In pursuit of this goal one may utilize experimental, interpolatory, or deductive techniques and combine them where feasible. If the approach is purely experimental a search is made for key pathways suggested by careful scrutiny of the census data. Such pathways are then explored under controlled conditions much as one would, for different reasons, conduct a simpler assay. Suppose the following hypothesis is framed on the basis of the earlier findings, namely: when the adult ratio of winning to losing species attains a certain value then production of the latter in succeeding generations is disproportionately reduced. It should then be possible to test the hypothesis with considerable realism by setting up replicated series of species-ratios (in A, of course) and assessing the natality and mortality responses assumed to lead to differential species survival. If the analytical data confirm the populational trends, the way is opened for the next experiment. If they are indifferent or contradictory a fresh start is required. This can be a slow and wasteful process. On the other hand, it may quickly lead to the mechanisms of primary significance and eliminate those which can thereafter be neglected. Both prior knowledge and intuition are helpful in this kind of attack.

Another technique is to work statistically with the original population data. This, to be successful, requires that every possible measure of natality and mortality is available, in time, for each life history stage. The investigator tries to describe all functional relations by, say, multiple-regression analysis. This procedure was adopted by Strawbridge [30] and, in a somewhat extended way, by Watt [32]. Findings derived from such analyses can be considered answers in their own right or they can be used as leads for further experiment.

Finally, as mentioned in the Introduction, one may again proceed analytically by erecting deterministic and/or indeterministic models based on assumptions regarding the underlying mechanism. This aspect comes in for later attention and no additional comment is needed here apart from stressing the point that the success of an adequate model lies in the degree to which it conforms with empirical reality.

In figure 2 the right-hand arrow describes a *populational* extension. The original finding of design A is reproduced but attention centers, not on causation, but on extension of the phenomenon to new conditions. In effect, the investigator asks two questions: (1) will interspecies competition exist in the new design and (2) if so, what pattern(s) will it assume? The diagram shows that, with a change from A to B, the action of competition is again proved (single-species controls being run in B, of course) but a *qualitatively* different result is obtained; the other species (broken-line) is the winner instead of the loser.

If we assume that design B has ecological realism, as we did for design A, we are in a position to generalize modestly:

(1) Competition can be detected through elimination of one species by the other (though other criteria are not excluded for other designs or species).

(2) The action of competition is not restricted to one design.

(3) One species is not exclusively superior in competition prowess to the other.

Such generalizations begin to acquire conceptual meaning for ecology! As they increase in number with increase in populational extensions, their meaning is enriched. This advance is not restricted to interspecies competition—an illustration we have stressed merely because we are closer to it in our own work. Comparable research can be done with models of different, but equally important, aspects of the "struggle for existence"—plant-herbivore, predator-prey, host-parasite, and mutualistic interactions.

(iii) *An empirical population experiment.* The objective of this section is to examine certain population findings about competition between *Tribolium confusum* and *Tribolium castaneum* in order to illustrate specifically certain points made earlier and to lay a background for the statistical discussion to follow. In short, we wish to sketch a type of laboratory program for which the model has been shown to be adaptable. The extremely few facts selected for inclusion here are reported in detail by Park [38], [43] and these publications can be consulted if further information is desired.

Suppose we had long since passed through an initial census-experiment of the sort abstracted in the top of figure 2 and, from this, had decided to extend the research populationally by addition of new ecological variables. This actually was done, the variables being the climatic-habitat "imposed by design" (figure 1). Temperature and humidity (relative) were chosen and these were combined factorially to yield the following six "treatments," 34°–70 per cent, 34°–30 per cent, 29°–70 per cent, 29°–30 per cent, 24°–70 per cent, and 24°–30 per cent. Into each of these climates replicated sets of populations were introduced consisting of *T. confusum* alone (controls), *T. castaneum* alone (controls), and an equal mixture of *T. confusum* and *T. castaneum* (competition-experimentals). There were 400 populations in all and every culture was observed and censused once per 30 day interval. At time of census the living stages were counted (except eggs), all were placed in a new vial containing eight grams of fresh flour, and then returned to the same moisture and heat conditions from whence they came. The cultures were handled exactly in this manner for a minimum of 26 censuses (or $26 \times 30 = 780$ days); some were continued for 62 censuses (1860 days). Analysis of these data permits the following questions to be answered:

What relation exists between the six temperature and humidity combinations and

(a) the census behavior of *T. confusum* populations;

(b) the census behavior of *T. castaneum* populations;

(c) the census behavior of the two species when both are competing in a shared habitat?

In answering the questions a mass of material has been reduced to the barest minimum and is summarized in table I. For convenience, we use the notations *b* and *c* to refer, respectively, to *T. confusum* and *T. castaneum*; and the Roman numerals I through VI to identify the six climates (I = 34°/70 per cent; II = 34°/30 per cent; III = 29°/70 per cent; IV = 29°/30 per cent; V = 24°/70 per cent, and VI = 24°/30 per cent). The first column of the table specifies the climatic habitats. The next two columns refer to single-species populations, namely, which species maintains greater, and which lesser, mean densities over the period of observation (column 2) along with the significance of the difference between each couplet (column 3). The lower-case letter identifies the species in column 2; the number following in parentheses its average total density per gram of flour. The last column pertains to events in competition cultures and lists *above* each horizontal line the species that usually, or always, wins and the percentage of those wins among the relevant array of replicates. Similar information for the species surviving less frequently (or not at all) appears *below* each horizontal line.

The first task is to summarize briefly the results obtained for single-species controls (table I). The primary point is that all populations persist successfully in all treatments with exception of *T. castaneum* in VI (24/30). This is the major conclusion. It permits us to ascribe the eliminations that occur in competition-cultures, not to the direct action of temperature and humidity, but rather to the *new* impact incorporated in the model when the two forms are forced to live together. Our next point is that, although control groups do maintain themselves, their *densities* are frequently affected by the physical conditions. This is true on either of two bases of comparison; within-species but between treatments, and between-species but within-treatments. For example, in every treatment except I (34/70) one species is superior to the other in respect of its sustained density. *T. confusum* is favored in II, IV, and VI; *T. castaneum,* in III and V. Only in I are the two forms evenly matched. Within-species comparisons can be derived from column 2 of table I but they are omitted here in the interest of brevity on the ground that they are not essential for the argument to follow.

TABLE I

Comparison of Single-species Densities with Species-elimination Patterns in Mixed Populations

Treatments	Single-species populations		Mixed-species populations
	Higher density Lower density	Probability	Usual winner (% wins) Occasional winner (% wins)
I	*b* (41) *c* (38)	> 5%	*c* (100%) *b* (none)
II	*b* (24) *c* (10)	< 1%	*b* (90%) *c* (10%)
III	*c* (50) *b* (33)	< 1%	*c* (86%) *b* (14%)
IV	*b* (50) *c* (19)	< 1%	*b* (87%) *c* (13%)
V	*c* (45) *b* (28)	< 1%	*b* (71%) *c* (29%)
VI	*b* (26) *c* (3)	< 1%	*b* (100%) *c* (none)

The interspecies aspects require more attention. There is, again, a major qualitative conclusion: one species *always* persists and the other species *always* is eliminated in every culture. This fact, clearly an expression of coassociation, holds true irrespective of temperature-moisture, and single-species, relations and leads to the assertion that competition is proved to be operating. But the results of competition are multifarious. It is in the frequency-pattern of the various eliminations that we discern elements of novelty—elements patently of significance both for the mathematical statistician and the ecologist. Let us pursue this.

We note, relative to treatment, two sorts of end-results of competition. In the first case one species is eliminated 100 per cent of the time while the other survives 100 per cent of the time. In the second case the consequences are "alternative"; *b* persists with a certain frequency as does *c*. Treatments I and VI characterize the first, and II, III, IV, and V, the second pattern. The disappearance of *T. castaneum* in VI, however, cannot be ascribed to "competition" since this species when husbanded by itself is unable to tolerate for many generations the imposed conditions of low-temperature and low-humidity. Therefore, we eliminate this example from further review.

It is instructive to consider by treatments the relation between density-levels sustained in control populations and species-eliminations in experimental populations. On *a priori* grounds one might logically argue that the species favored as a control would be still favored when in competition. Table I permits this hypothesis to be examined. Take the case of treatment I. Here, the climatic habitat is equally adapted to both beetles. The expectation might well be that, on coassociation, *b* would win in approximately one-half, and lose in approximately one-half, of the replicates. Yet this does not occur; *c* is the exclusive winner. In short, competition adds an impact over and above the control performance which leads to invariable extinction of *b*.

Consider treatments II, III, and IV. Species considerations aside, these afford the best generalization of the research for the reason that their pattern is alike (I, V, and VI all being different). Within these treatments the consequences are alternative and occur with similar frequency. In controls, one beetle shows a definite superiority (column 2) and this species survives significantly more than 50 per cent of the time in living with its rival (column 4). But the control trend can be contradicted nevertheless and this actually happens in a small proportion of the instances.

Finally, there is the interesting situation in V which departs from all others. When living apart, *T. castaneum* maintains a mean density of 45 beetles per gram and *T. confusum* of 28 per gram. The latter is only about two-thirds the number of the former and the difference cannot be explained on the hypothesis of even chance. The point, however, is that *T. confusum* is the *usual* survivor in the presence of a competitor "presumed" to be favored on the basis of single-species performance!

It is evident that there is an element of "empirical indeterminism" among the replicates comprising the competition cultures of II, III, IV, and V. This is to say, the dependence of the survival of a species on the characteristics of its environment appears to have the nature of a chance event, though not a 50–50 event. From this point of view some generality might be gained by considering the survival of a given species always as a chance event with variable probability, P, of survival where, on occasion, P may be unity or zero. The intent of this statement is not to deny or discard the utility of the "analytical approach" in study of causation but, rather, to set the stage for the probabilistic considerations about to follow.

This aspect finds empirical illustration in the two accompanying figures. In figure 3 the abscissa is number of *T. confusum* adults per vial; the ordinate, *T. castaneum*. A single point within the coördinates jointly describes the number of both at a particular census. As the points move toward the ordinate *T. confusum* decreases; toward the abscissa, *T. castaneum*. Two cultures from V have been consciously selected in illustration. In figure 3 the broken line is a history eventually leading to elimination of *T. castaneum*. The solid line describes the elimination of *T. confusum*. There is an interval in earlier phases when each replicate engages in what might be termed "random walk." It can be seen that the two lines intercross despite eventual opposite outcomes. In fact the relations

$b > c$, but b becoming extinct;
$c > b$, but c becoming extinct;

though transitory, are evident. However, once either of the black diagonal lines is crossed such relations disappear and a point of no return is reached.

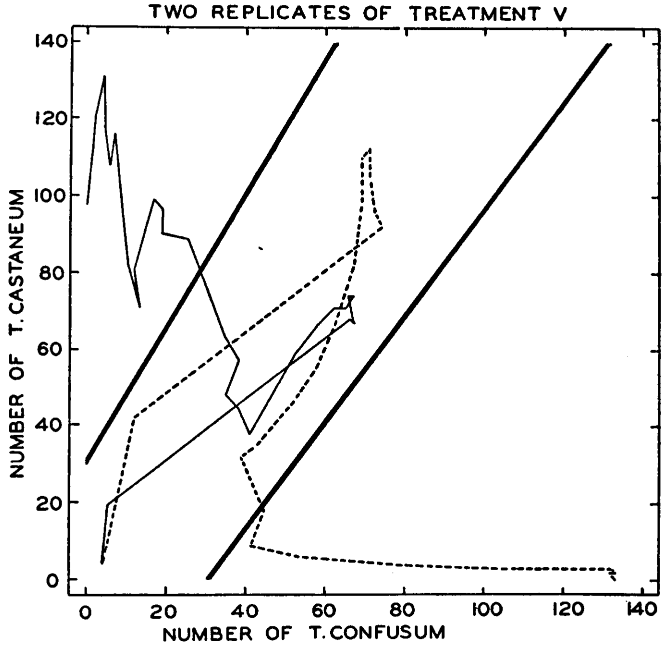


FIGURE 3

Number of *T. castaneum* adults plotted against number of *T. confusum* adults. Two replicates chosen from treatment V. Solid line is *T. confusum* eliminated; broken line, *T. castaneum.*

Suppose we ignore treatment I in which consequences are "deterministic" in the sense that *T. castaneum* always wins. Suppose further we fail to identify the individual replicates and their census-age. Then, we construct another diagram with axes like those of figure 3 in the following way. We begin with replicate 1 of treatment II. If *T. confusum* eventually is to disappear we adopt, say, the convention of a cross; if *T. castaneum*, a circle. Next, we plot the number of both species for that replicate until one number reaches zero. The remaining replicates are graphed in the same way. A new diagram is started for treatment III and this process is continued until all treatments have been plotted. When the four diagrams are finished we visually draw two "barriers" for each. These barriers enclose a zone of mixed-species numbers within which both crosses and circles are contained. Outside the left barrier only crosses remain, and outside the right barrier, only circles. The results appear as figure 4 in which the empirical percentage eliminations are shown as directional arrows.

The figure depicts for each of the four alternative treatments an indeterministic zone, within which an elimination can proceed in either way though *not* with equal probability, and two deterministic zones where only one consequence is possible. This, clearly a probabilistic situation when viewed for the *total array* of comparable replicates, mandates that any realistic deductive modeling of the data must take stochastic form. It is interesting to note that the barriers, as well as the probabilities, change with the temperature-humidity habitat—a matter well illustrated by figure 4.

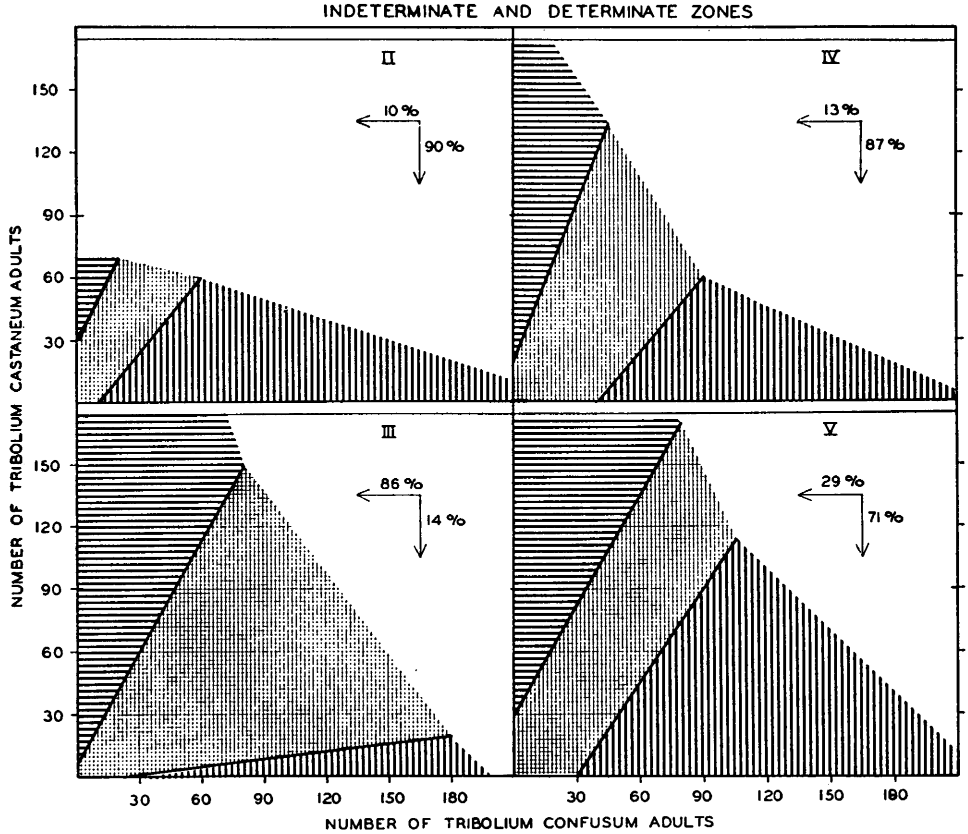


FIGURE 4

Indeterminate and determinate zones empirically computed for treatments II, III, IV, and V. See discussion in text.

A final point occurs. Are the species-elimination patterns reproducible? It is, of course, impractical to answer this on the basis of much evidence since competition experiments of this type require many months and much labor for completion. However, one segment of evidence does exist for treatment III (29/70). Park [37] competed the two species in this physical habitat and Kennington [49] did likewise. The first report had *T. castaneum* the victor in 12 of 18 replicates (67 per cent); the second, in 19 of 20 replicates (95 per cent). Pooling these results with those reported in table I and gaining thereby the impressive replication of 66 cultures (18 + 20 + 28), it is seen that in 55 instances *T. castaneum* survives (83 per cent) to be contrasted with 11 instances (17 per cent) for *T. confusum*. Thus, though the percentages differ somewhat, the facts remain (a) that the events are truly "alternative" in the sense defined and (b) that *T. castaneum* is the usual survivor.

This concludes our discussion of the biological aspect of the *Tribolium* model and we now turn to the purely statistical aspect.

PART II. STATISTICAL ASPECTS

4. Introductory remarks

In the present, several years old, cooperation in the study of competition between two species of *Tribolium*, the statistical-theoretical efforts were directed toward the invention of a chance machinery, or of a stochastic model, for the phenomena described in the first part of this paper, which could adequately represent (or "explain") the experimental results. The models contemplated can be conveniently classified on two different bases and the present introductory remarks are concerned with these two classifications.

First we shall distinguish between models of statistical interaction between organisms and environment and models of biological interaction. Models of statistical interaction are characterized by the postulated lack of influence of the environment on the biological properties of the organisms studied. On the other hand, models of biological interaction involve postulates describing the changes in the biology of the organisms ascribed to the influence of the environment. One example must suffice to illustrate this distinction. As is well known, the net fecundity of *Tribolium* depends on crowding. If eight pairs of beetles are left for 24 hours in flour, then at the end of this period the vial may contain as many as 46 eggs. But 32 pairs of beetles, on the other hand, may produce a total of 156 eggs. The rate per female at the lower density is higher than that at the higher density; approximately 12 eggs as compared with 10. An attempt to explain this difference, which becomes greater with larger densities, may be of two kinds. First it may be assumed that in both cases the beetles have the same biological characteristics so that, with the unavoidable chance variation from one female to another, they lay the same number of eggs per unit of time, depending on the age of the beetles, on the temperature, the humidity, etc. Also, a fixed mechanism of searching for food and cannibalism of the eggs may be assumed. With this scheme, the observable difference in net fecundity would be ascribed to the relatively greater success the beetles have, when there are more of them in the vial, in searching for and eating the deposited eggs. A model of this kind is what we call the model of statistical interaction between the given species of beetles and crowding. Obviously, it is natural to begin a study with models of statistical interaction. If and when these models fail to account for all the details of the phenomena, it is equally natural to resort to models of the other kind, postulating changes in the biology of the organism considered. Thus, for example, a model of the second kind may postulate that to each density of beetles in a vial there corresponds a different distribution of the number of eggs laid by a female of a given age. A model depending on such postulates will be called a model of biological interaction.

The authors are inclined to adhere to the rule of Occam ("Occam's razor") of scientific studies, to the effect that *principia non sunt multiplicanda preter necessitatem* and favor models of statistical interaction so long as they conform with realities. Also, they are aware of the fact that, in order to substantiate a model of biological interaction, failures of several attempted statistical models are not sufficient and a recourse to some physiological experimentation is necessary.

Our second distinction between models will be on the basis of whether they are "in the small" or "in the large." Whatever the substantial class of phenomena may be, there is always an element of this class, that we may call the primary element or the primary phenomenon that attracts particular attention and appears of a greater interest than the others, which we may label secondary. Also, invariably, the primary element of a class of phenomena is connected with a great number of others. In fact, in many instances, the primary phenomenon is, so to speak, the final outcome of a great many interacting secondary phenomena.

A comprehensive model of the whole class of phenomena may be expected to represent all of them, the primary as well as the secondary ones. However, a comprehensive model of this kind is, of necessity, extremely complicated and may be only an ideal and a goal for the efforts of generations of scientists. Models of frequent occurrence do not attempt to represent the whole class of phenomena studied but only its separate sections. In particular, we frequently attack the primary phenomenon and try to build its "summary" model or its model "in the large" based on relatively few simplifying assumptions which ignore a great number of details but are meant to emphasize the role of several factors deemed to be of predominant importance. In parallel with these models "in the large" we build models meant to represent secondary phenomena in the given class. Ordinarily, these particular models are characterized by an effort at a deeper study and their basic postulates concern the details which are ignored in the summary models. These models concerned with secondary phenomena will be called the models "in the small."

Naturally, the question as to which of the phenomena considered are the primary and which are the secondary is somewhat subjective and depends on the point of view of the scientist concerned.

Out of the wealth of experimental material produced at the Hull Zoological Laboratory the outstanding and most interesting phenomena may be reviewed again as follows.

(i) If allowed to live alone, each of the two species of *Tribolium* appears capable of maintaining indefinitely reproducing populations (with the one exception of treatment VI discussed earlier).

(ii) If forced to live together, one of the two species invariably dies out.

(iii) Under certain environmental conditions, the identity of the surviving species varies from one replicate of the experiment to the next.

(iv) Finally, the more frequent winner in this struggle for survival is, occasionally, the species which, living alone in the given conditions, maintains a lesser population density than the losing species.

In the present studies this particular phenomenon is treated as the primary phenomenon and as the one of greatest ecological significance. Obviously, this phenomenon is an "outcome" of a great many other phenomena, such as the duration of the various phases of the life cycles of the two species (egg, larva, pupa, adult), their fecundities, their voracities, and also the biological reactions of these species to crowding and to contacts with each other. All these other phenomena are treated as secondary.

All the models thus far studied theoretically-statistically are concerned with statistical interactions only. Two of them, one studied by Dr. Lucien Le Cam, are models in the large of the primary phenomenon of interaction between the two species. In an effort at a better understanding of the development of the population of beetles, several models in the small were studied. In this the authors had the benefit of cooperation of Dr. C. L. Chiang and of Dr. Bernard Sherman. It is anticipated that the details of these studies will appear in separate publications. The following sections give an over-all summary of the results obtained.

5. General result based on the theory of Markoff processes

An attempt to construct a model "in the large" of the apparent phenomenon of a state of equilibrium of a single species was made by Le Cam, as follows.

Suppose that the life cycle of a beetle can be divided into a finite number m of different "states," say $A_1, A_2, \cdots, A_m$. When an egg is laid then this egg is considered as a beetle in state A_1. A_2 may denote a particular phase in the life of an egg, etc. A_m represents the final phase in the life of an adult beetle. The specific assumptions adopted are:

(a) The beetles can be born only in state A_1.

(b) While in any state A_k, at any moment t, a beetle can either continue to stay alive in A_k or it can die or, if $k < m$, can pass to the next state A_{k+1}.

In accordance with the above, at any moment t the state of a population of beetles in a vial can be characterized by a set of m nonnegative numbers $n_1, n_2, \cdots, n_m$ which we shall denote by a single symbol $x(t)$. Here n_k denotes the number of beetles in the vial which at moment t are alive and in state A_k.

The assumptions (a) and (b) refer to the classification of phases of life of a beetle and the description of the state of their population. Now, we proceed to the specifically probabilistic assumptions. In the simplest form of the model the main point of these assumptions is that the probabilities of any changes in a population within an infinitesimal interval of time, from t to $t + dt$ are determined by the state $x(t)$ of the population at the moment t. More specifically, it is assumed as follows.

(c) The probability of an infinity of changes in the population during any finite interval of time is zero. The probability of more than one change during the time interval (t_1, t_2) tends to zero faster than the length $t_2 - t_1$ of this interval.

(d) To every interval of time $(t, t + dt)$ there correspond the following probabilities:

The probability that one egg will be laid in $(t, t + dt) = \beta(x)dt + o(dt)$,

The probability that one beetle in state A_k for $k = 1, 2, \cdots, m$ will die during $(t, t + dt) = \gamma_k(x)dt + o(dt)$,

The probability that one beetle in state A_k with $k = 1, 2, \cdots, m - 1$ will pass to the next state $A_{k+1} = \delta_k(x)dt + o(dt)$.

Here it is assumed that $\beta(x) \geqq 0$ and $\gamma_k(x) > 0$, $\delta_k(x) > 0$. Naturally, the definition of $\gamma_k(x)$ and $\delta_k(x)$ requires that at time t the class A_k contain at least one beetle.

Under the above hypotheses, the theory of Markoff processes, as developed by Paul Lévy and others, implies that, over an infinite period of time the population of beetles must either die out or grow to infinity. The probabilities of these two possible outcomes, α and $1 - \alpha$, respectively, are computable from the functions $\beta(x)$, $\gamma_k(x)$ and $\delta_k(x)$.

This conclusion persists if the functions $\beta(x)$, $\gamma_k(x)$, $\delta_k(x)$, assumed to depend only on the state x of the population, are replaced by products of such functions multiplied by periodic functions of time. These periodic factors depending on time may be visualized as representing the effects of the periodic censuses of beetles, accompanied by a change in the flour in which the beetles live.

The comparison of the above results with the experiments leads to the following conclusions: either the instantaneous probabilities of laying eggs, of passing from one phase in the life cycle to the next and the probabilities of death of beetles cannot be assumed to depend solely on the state of the population and, periodically, on time, but must be postulated to depend on the history of the population leading to its state at a given moment, or else the period of observations, long as it is, is still "too far from infinity" for the phenomenon of the dying out of the populations to be observable. As things stand now, the authors may offer only their guess in favor of the second alternative. Incidentally, under one particular treatment, (VI), the single-species populations of *Tribolium castaneum* were actually observed to die out invariably, after a shorter or longer period of struggle for survival (see Part I).

6. Discrete generations model of competition between two species

In the present section we outline a model "in the large" of the primary phenomenon of struggle for existence as described in section 4. The general idea behind this model is that the four points describing the primary phenomenon, (i) through (iv), depend predominantly on the following factors.

(a) In conditions of temperature and humidity in which the two species of *Tribolium* appear to survive indefinitely, the number ν of eggs laid by each female of either species during her lifetime is large, of the order of magnitude of 1000.

(b) The conditions of temperature and humidity being fixed, the two species of *Tribolium* differ in the average values of ν. Also, there is a substantial variation of ν from one female of a given species to the next.

(c) In the fixed conditions of temperature and humidity, the two species of *Tribolium* differ in their voracity (this is a term to be defined later).

(d) That in the same fixed conditions the two species differ in the duration of the two passive phases of their life cycle, the egg and the pupa.

(e) That the active forms of *Tribolium*, the larva and the adult eat the two passive forms, the egg and the pupa, whenever they have an opportunity.

In constructing the model, an effort was made to treat the above factors realistically. On the other hand, mathematical difficulties created the necessity of various far-reaching simplifications concerning a number of other details in the development of a population.

The first simplification consists in ignoring the distinction between the two passive (egg and pupa) and the two active forms (larva and adult). Thus, instead of organisms with four successive phases of the life cycle, we shall consider hypothetical beetles with only two phases, one passive, to be labeled "egg," and the other active, to be labeled "adult." Two species of these hypothetical beetles will be considered. It will be assumed that to the ith species, $i = 1, 2$, there corresponds a fixed period of time τ_i during which an egg of this species turns into an adult.

Our next simplification consists in ignoring the distinction between the sexes. All the hypothetical beetles are assumed to lay eggs. The number of eggs laid by a beetle of the ith species will be denoted by ν_i and treated as a random variable independent of the number of eggs laid by any other beetle and following a fixed distribution with the probability generating function $G_{\nu_i}(t)$ with finite moments, at least up to the second order.

The greatest simplification adopted consists in replacing the gradual change of generations of *Tribolium* by a discontinuous one. An adult *Tribolium* female lays eggs over a period of roughly about 150 days. On the other hand, the time elapsed from the laying of an egg to its turning into an adult is only about 30 days. It follows that in a population allowed to develop for a substantial time there will be present representatives of several succeeding generations.

Instead of this mixing of generations we will assume that the hypothetical beetles have "seasonal" life cycles. This requires the division of time into successive "seasons," $S_0, S_1, \cdots, S_n, \cdots$. The hypothetical experiment starts at the beginning of the "zero season" S_0 when x_0 new-born adult beetles of the first species and y_0 new-born adult beetles of the second are put into the vial. These beetles form the "original" generation. It is assumed that at the beginning of S_0 each beetle lays all its eggs. Thereafter each egg is exposed to the risk of being eaten by any of the $x_0 + y_0$ beetles of both species present in the vial. The duration of this risk for an egg of the ith species is τ_i. If an egg survives this risk, then it turns into an adult representative of the first generation born. This may happen before the conclusion of the original season S_0. However, it will be assumed that until S_0 ends, the members of the first generation born remain "dormant," do not lay their eggs and do not cannibalize. These two functions begin at the start of the next season S_1, etc. In general, it is assumed that all adult beetles born during the ith season S_n begin to function at the start of the $n + 1$st season S_{n+1}, when they lay their eggs. Thereafter, all of them live through S_{n+1}, looking for eggs and eating them.

Now there remains to enumerate the hypotheses regarding cannibalism. These hypotheses are the usual ones adopted in similar studies.

(1) To any specified egg E, to any period of time (t_1, t_2) preceding the time when this egg can turn into an adult and to any beetle of the ith species, $i = 1, 2$, there corresponds a conditional probability, given that this egg survives up to the time t_1, that the beetle under consideration will find and eat the particular egg, namely

$$p_i(t_1, t_2) = \mu_i(t_2 - t_1) + o(t_2 - t_1) \tag{1}$$

where the coefficient μ_i is a constant characterizing the "voracity" of the ith species, for $i = 1, 2$.

(2) The beetles present in the vial search for eggs independently. Thus, given that the egg E survives up to time t_1, the probability that m_1 beetles of the first species and m_2 of the second will all fail to find the egg E during the time interval is equal to

$$[1 - p_1(t_1, t_2)]^{m_1}[1 - p_2(t_1, t_2)]^{m_2} . \tag{2}$$

(3) Given that several specified eggs survive up to time t_1, their fates during the subsequent period of time (t_1, t_2) are mutually independent.

Starting with the above three postulates and following the familiar pattern of reasoning [50] it is now easy to deduce that, given that the nth generation of beetles in a vial contains exactly x_n adults of the first species and exactly y_n adults of the second, the probability $\theta_i(x_n, y_n)$ that a given egg in this vial, laid by a beetle of the ith species will survive the prescribed period τ_i and will become an adult of the $(n + 1)$st generation is given by

$$\theta_i(x_n, y_n) = e^{-(\mu_1 x_n + \mu_2 y_n)\tau_i}, \qquad \text{for i} = 1, 2 . \tag{3}$$

Now consider an experiment which consists in putting into a vial, with a suitable amount of flour and kept under fixed conditions of temperature and humidity, a certain number x_0 of beetles of the first species and a certain number y_0 of the second, and letting them develop a sequence of generations in conditions described above. Denote by X_n and Y_n the numbers of beetles of the two species born in the nth generation. In order to obtain an idea of the implications of the model described, it will be our purpose to deduce the conditional distribution of X_{n+1} and Y_{n+1}, given that X_n and Y_n have assumed some specified values x_n and y_n, respectively. This distribution will be characterized by the joint probability generating function, denoted by $G_{n+1}(t_1, t_2 | x_n, y_n)$.

Denote by $X_{n+1}(j)$ and $Y_{n+1}(j)$ the numbers of adults in the $(n + 1)$st generation which are descendants of the jth individuals of either species of the nth generation. Obviously

$$X_{n+1} = \sum_{j=1}^{x_n} X_{n+1}(j) , \quad Y_{n+1} = \sum_{k=1}^{y_n} Y_{n+1}(k) . \tag{4}$$

The postulates adopted in the model imply that all the variables $X_{n+1}(j)$ and $Y_{n+1}(k)$ are completely independent. Also all the $X_{n+1}(j)$ are identically distributed for $j = 1, 2, \cdots, x_n$. Similarly, the $Y_{n+1}(k)$ are also identically distributed. It follows that, if we denote $g(t_1)$ and $h(t_2)$ the probability generating functions of $X_{n+1}(j)$ and $Y_{n+1}(k)$, respectively, then

$$G_{n+1}(t_1, t_2 | x_n, y_n) = g^{x_n}(t_1) h^{y_n}(t_2) . \tag{5}$$

Now we evaluate $g(t_1)$ and then write the formula for $h(t_2)$ by analogy. We have

$$g(t_1) = E[t_1^{X_{n+1}(j)}] = E\{E[t_1^{X_{n+1}(j)} | \nu_1]\} \tag{6}$$

where ν_1 stands for the number of eggs laid by the jth beetle of the first species, member of the nth generation. If ν_1 has a fixed value m, then $X_{n+1}(j)$ is a binomial variable with exponent m and with the probability of "success" equal to $\theta_1(x_n, y_n)$. Thus, the conditional probability generating function of $X_{n+1}(j)$, given $\nu_1 = m$, is

$$[1 - \theta_1(x_n, y_n) + t_1 \theta_1(x_n, y_n)]^m . \tag{7}$$

Using formula (6) we may now write

$$\begin{aligned} g(t_1) &= \sum_{m=0}^{\infty} P\{\nu_1 = m\} [1 - \theta_1(x_n, y_n) + t_1 \theta_1(x_n, y_n)]^m \\ &= G_{\nu_1}[1 - \theta_1(x_n, y_n) + t_1 \theta_1(x_n, y_n)] . \end{aligned} \tag{8}$$

The formula for $h(t_2)$ is obtained from the right-hand side of (8) by substituting ν_2, θ_2 and t_2 for ν_1, θ_1 and t_1, respectively. Formula (5) gives then

$$(9) \quad G_{n+1}(t_1,\ t_2|x_n,\ y_n) \\ = \{G_{\nu_1}[1-\theta_1(x_n,\ y_n)+t_1\theta_1(x_n,\ y_n)]\}^{x_n}\{G_{\nu_2}[1-\theta_2(x_n,\ y_n)+t_2\theta_2(x_n,\ y_n)]\}^{y_n} .$$

Using (9) it is now easy to obtain the conditional expectations $\xi(x_n,\ y_n)$ and $\eta(x_n,\ y_n)$ of X_{n+1} and Y_{n+1}, respectively, and also the conditional variances of these variables, say $\sigma_1^2(x_n,\ y_n)$ and $\sigma_2^2(x_n,\ y_n)$, respectively. We have

$$(10) \qquad \xi(x_n, y_n) = \bar{\nu}_1 x_n \theta_1(x_n, y_n) \quad \text{and} \quad \eta(x_n, y_n) = \bar{\nu}_2 y_n \theta_2(x_n, y_n)$$

where ν_i represents the expectation of ν_i, and

$$(11) \qquad \sigma_1^2(x_n,\ y_n) = \bar{\nu}_1 x_n \theta_1(x_n,\ y_n)\left[1 - \left(1 - \frac{\sigma_{\nu_1}^2}{\nu_1}\right)\theta_1(x_n,\ y_n)\right]$$

with an analogous formula for $\sigma_2^2(x_n,\ y_n)$. Here $\sigma_{\nu_i}^2$ represents the variance of ν_i. Ordinarily this variance is substantially smaller than $\bar{\nu}_i$.

Now we shall use formulas (10) and (11) in order to show that the model constructed involves a self-regulating machinery, whereby each of the two species cultured alone tends to maintain a population of a size fluctuating about a certain point of equilibrium. Also, it will be shown that, if both species are cultured together, then one of them will tend to die out, leaving the field to the other.

Our first remark is that formulas (10) and (11), combined with the assumption that $\sigma_{\nu_i}^2 < \bar{\nu}_i$, imply

$$(12) \qquad \frac{\xi(x_n,\ y_n)}{\sigma_1(x_n,\ y_n)} > \{\xi(x_n,\ y_n)\}^{1/2} .$$

It follows that, whenever $\xi(x_n,\ y_n)$ is substantial, the probability that X_{n+1} will be equal to zero is small. A similar conclusion applies to Y_{n+1}.

Next we consider the case where $y_0 = 0$ and, therefore, $y_n = 0$ and study the dependence of $\xi(x_n,\ 0)$ on x_n. Using formula (3), we obtain

$$(13) \qquad \xi(x_n,\ 0) = \bar{\nu}_1 x_n e^{-\mu_1 \tau_1 x_n} .$$

Using elementary methods it is easy to establish that formula (13) has the following properties. The expectation $\xi(x_n,\ 0)$ has a maximum value

$$(14) \qquad \max \xi(x_n,\ 0) = \frac{\bar{\nu}_1}{\mu_1 \tau_1 e}$$

which is reached when $x_n = 1/\mu_1\tau_1$. Thus, whatever may be the number x_n of adults in the vial counted at the end of the nth season, the expected number of adults during the next season can never exceed the limit (14). This explains why in the experiments conducted the populations of isolated species never showed a tendency to increase indefinitely. Further, the expectation $\xi(x_n,\ 0)$ of X_{n+1} exceeds the value of x_n only in those cases when

$$(15) \qquad x_n < \frac{\log \bar{\nu}_1}{\mu_1 \tau_1} = \epsilon_1, \quad \text{say}.$$

Also, the expectation of X_{n+1} will be less than x_n in all cases when

$$x_n > \epsilon_1 . \tag{16}$$

These conclusions indicate that, apart from the unavoidable random variation, the numbers of individuals in the successive generations of the first species, when husbanded separately from the other species, will tend to fluctuate about the value of ϵ_1 which may be termed the point of equilibrium. If ϵ_1 is substantial then the probability of dying out will be small. Naturally this conclusion holds good for the second species as well as for the first and explains the point (i) of the description of the primary phenomenon contemplated.

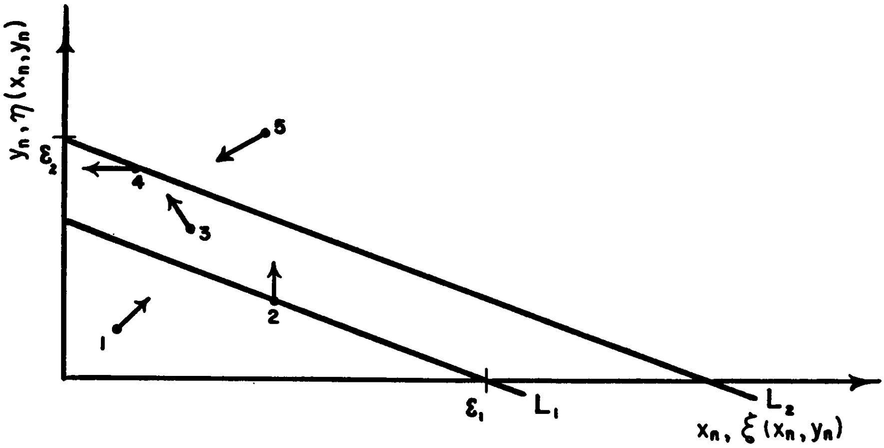


FIGURE 5
Geometrical interpretation of statistical intersection between two species.

Now we proceed to the study of the development of a mixed population of beetles, originally composed of both species. Thus $x_0 > 0$ and $y_0 > 0$. If, for any n, one of values x_n or y_n is equal to zero, then the reasoning in the preceding lines would apply and the conclusion will be that the surviving species will tend to fluctuate about its particular point of equilibrium. Therefore, all that remains is to investigate the case where both x_n and y_n are some positive numbers.

Following the lines of analysis indicated above, we seek the conditions under which the expectation $\xi(x_n, y_n)$ is greater than x_n. Using (3) and (10), we have

$$\bar{\nu}_1 x_n \theta_1(x_n, y_n) > x_n , \tag{17}$$

or

$$\mu_1 x_n + \mu_2 y_n < \frac{\log \bar{\nu}_1}{\tau_1} = \mu_1 \epsilon_1 . \tag{18}$$

Conversely, if the left-hand side of (18) is greater than $\mu_1 \epsilon_1$ then the expectation of X_{n+1} will be less than x_n. Similarly, in order that the expectation $\eta(x_n, y_n)$ of Y_{n+1} be greater than y_n, it is necessary and sufficient that

$$\mu_1 x_n + \mu_2 y_n < \frac{\log \bar{\nu}_2}{\tau_2} = \mu_2 \epsilon_2 . \tag{19}$$

From this point on it will be convenient to interpret the situation geometrically. In figure 5 the quantities measured on the horizontal axis are x_n and $\xi(x_n, y_n)$. Those measured on the vertical axis are y_n and $\eta(x_n, y_n)$. The two parallel lines L_1 and L_2, to be termed lines of indifference, intersecting both axes, correspond to the equations

$$\mu_1 x_n + \mu_2 y_n = \mu_i \epsilon_i \quad \text{for } i = 1, 2 \tag{20}$$

and it is assumed that

$$\mu_1 \epsilon_1 < \mu_2 \epsilon_2 . \tag{21}$$

It will be seen that the lower line, corresponding to the first species, intersects the horizontal axis at $x_n = \epsilon_1$ and that the upper line, corresponding to the second species, intersects the vertical axis at $y_n = \epsilon_2$. Here it is assumed that

$$\epsilon_1 > \epsilon_2 \tag{22}$$

so that the equilibrium point of the first species is higher than that of the second. According to the inequality (18), whenever the point (x_n, y_n) lies below L_1, the expected value of X_{n+1} is greater than x_n, and vice versa. Similarly, according to (19), whenever the point (x_n, y_n) lies below the line L_2, the expectation of Y_{n+1} is greater than y_n, and vice versa. Thus if (x_n, y_n) lies below L_1, then both X_{n+1} and Y_{n+1} are expected to be larger than the values of x_n and y_n, respectively. This is indicated in figure 5 by an arrow starting from a dot marked 1. This arrow points towards the expected direction of a change in the population of beetles starting from point 1. Now, assume that the point (x_n, y_n) lies anywhere on the line L_1, for example in the position marked by the numeral 2. Now the expected value of X_{n+1} coincides with x_n. However, since the starting point (x_n, y_n) is still below the line L_2, the expectation of Y_{n+1} will be greater than y_n. Thus, as marked in figure 5, the expected change in the composition of the population is along a vertical line upwards. The next possibility is that the starting point (x_n, y_n) is anywhere in between the lines L_1 and L_2, for example at the point marked by the numeral 3. Since this point is above L_1 and below L_2, the expected change in the number of adults of the first species is a decrease and the expected change in the number of the second is an increase. This is reflected in the direction of the arrow starting from point 3. If the point (x_n, y_n) is exactly on the line L_2, as in the position of the point marked 4, then $\xi(x_n, y_n) < x_n$ and $\eta(x_n, y_n) = y_n$. Accordingly, the arrow attached to the point 4 is horizontal and is directed to the left. Finally, if (x_n, y_n) is above the line L_2, then the theory predicts a decrease in the numbers of both species. This is illustrated by the arrow attached to the point marked by the numeral 5.

Summarizing these results, we come to the conclusion that, wherever may be the initial position of the point (x_0, y_0) characterizing the original generation, provided both $x_0 > 0$ and $y_0 > 0$, the changes from one "season" to the next expected under the statistical interaction of the two species visualized in the model, will tend to drive the point (X_{n+1}, Y_{n+1}) into the band between the two lines L_1 and L_2 and thence toward the vertical axis in figure 5. But the vertical axis means the extinction of the first species. Once this is achieved, the second species will have the field to itself, and is expected to fluctuate about its own equilibrium point at ϵ_2. It will be seen that, with the constants selected to illustrate the situation in figure 5, the winning species is the second species whose equilibrium point ϵ_2 is less than the equilibrium point ϵ_1 of the losing species.

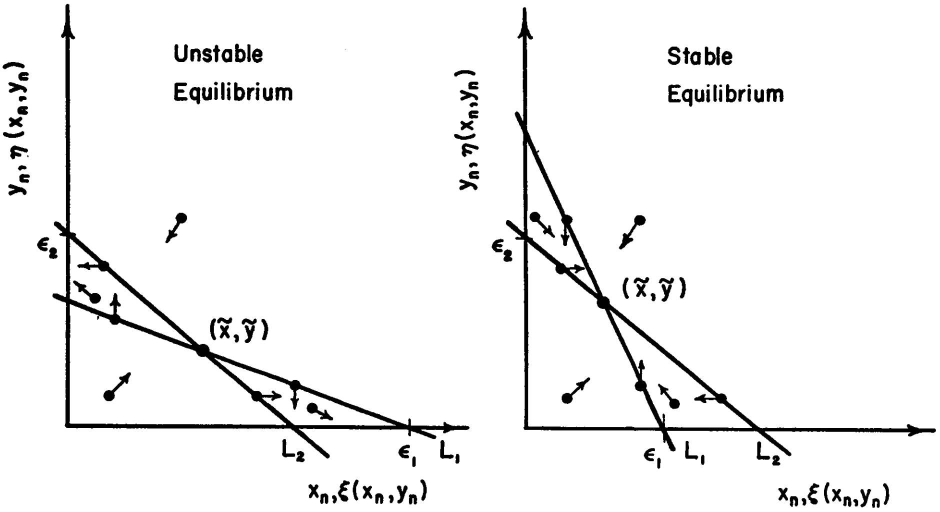
Note added in September, 1955. Equation (9) and figure 5 were discussed at the Symposium on Quantification in Population Ecology held in East Lansing on September 8, 1955. On this occasion Professor Leo Katz asked whether it is possible for the lines of indifference, L_1 and L_2, to cross.

The theory given here is based on the assumption that the two species of *Tribolium* eat each other's eggs, as well as their own, indiscriminately. However, theoretically, this need not be true, in which case, instead of parameters μ_1 and μ_2 characterizing the voracity of the two species, it is necessary to consider four parameters μ_{ij} for $i, j = 1, 2$. With this assumption, formula (3) for the probability that, in the presence of x_n adults of the first species and of y_n adults of the second, an egg of the ith species will survive to produce an adult will become

$$\theta_i(x_n, y_n) = e^{-(\mu_{1i}x_n + \mu_{2i}\, y_n)\tau_i}$$

for $i = 1, 2$. This, in turn, will lead to the following equation if the line of indifference of the ith species

$$\mu_{1i}x_n + \mu_{2i}y_n = \epsilon_i\mu_{ii}\,.$$



It will be seen that now the two lines L_1 and L_2 may cross. The point of intersection, say $(\tilde{x}, \tilde{y})$, may lie either within the positive quadrant exhibited in figure 5 or outside. Simple reasoning, facilitated by contemplating figure 5, indicates that the second of these two cases does not involve any essentially new elements. As to the first, it presents two possibilities exhibited in the accompanying figure with two panels. In both cases $(\tilde{x}, \tilde{y})$ represents the point of equilibrium. In the case treated in the left-hand panel, the equilibrium is unstable so that one or the other of the two species will become extinct. The proportion of cases in which a particular species becomes extinct depends on the values of x_n and y_n. In the case treated in the right-hand panel, the equilibrium is stable. The conditions necessary and sufficient for a stable equilibrium are

$$\frac{\mu_{21}}{\mu_{11}} < \frac{\epsilon_1}{\epsilon_2} < \frac{\mu_{22}}{\mu_{12}}\,.$$

These inequalities imply that at least one of the two species prefers its own eggs to those of the other species. Of course, the words "stable equilibrium" must be taken with a grain of salt. What is meant is that, under the conditions stated, the point representing the composition of the mixed population will fluctuate about the point $(\tilde{x}, \tilde{y})$.

Returning to the inequalities (18) and (19), it will be seen that the criterion deciding the outcome of the struggle for survival of the two species is the product, say C_i ,

$$C_i = \mu_i \epsilon_i \tag{23}$$

of the measure of voracity μ_i and the equilibrium point of a given species. In particular, if the two species husbanded in isolation are capable of maintaining the same level of equilibrium, the more voracious species is favored as a winner—a somewhat depressing conclusion morally. The criterion C_i may also be given another form obtained from (21) by substituting into it the expression of ϵ_i from (15),

$$C_i = \frac{\log \bar{\nu}_i}{\tau_i} . \tag{24}$$

The above explains the apparent paradox that a seemingly more vigorous species, capable of maintaining a higher approximately stabilized population, may be a consistent loser in competition. There remains to explain the fact that, under certain experimental conditions, a species of *Tribolium* is a frequent loser but not a one hundred per cent consistent loser. This may be explained qualitatively, as every thing else in the present section, by reference to figure 6 exhibiting the variation in the point of equilibrium of either species as observed in particular replicates of the experiments.

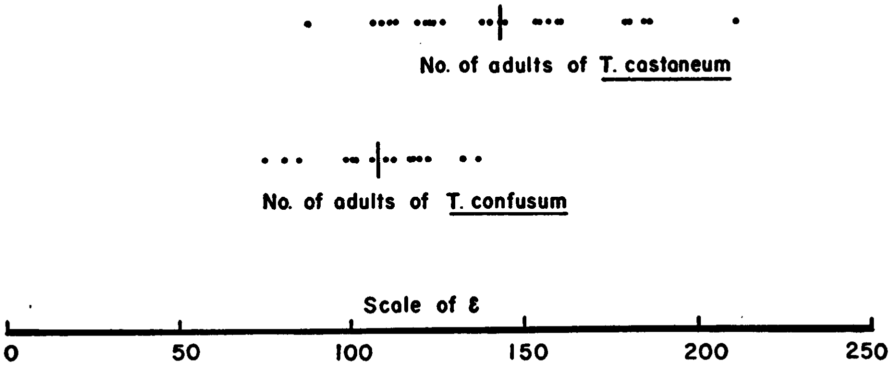


FIGURE 6

Variation in the point of equilibrium for control replicates under treatment III.

Unfortunately at present no reliable estimates exist for the voracity measures μ of the species in all the different conditions covered by the experiments on competition. Therefore, it is impossible to judge how much the values of the survival criteria C may vary from one replicate to the next. However, the variation of the equilibrium points exhibited in figure 6 suggests strongly that the values of the criterion C will also vary from one replicate of the experiment to the next and that, therefore, depending on the chance variation, the winning of the competition of one group of *T. confusum*, opposed by a particular group of *T. castaneum*, may well be observed along with the opposite result of the competition of two other groups of beetles.

As mentioned at the outset, the purpose of this section is to build a model *in the large* of statistical competition or interaction of two species of beetles. Therefore, certain aspects of the development of the populations were treated with very far-reaching simplifications. Essentially, no more than a qualitative agreement between the implications of the model and the results of the observation may be expected. Nevertheless, it appears interesting to compare the qualitative predictions drawn in the analysis of figure 5 with the curves illustrating the actual observations on the competition between the two species of *Tribolium*. These curves, termed competition curves, are given in six panels of figure 7, each corresponding to a separate treatment (see Part I). In each case, the quantity measured on the horizontal axis is the number of *T. confusum* adults. The quantity measured on the vertical axis is the number of adults of *T. castaneum*. The vertices of the polygons drawn correspond to the observations at successive censuses of the beetles, made at 30-day intervals. Whenever a particular species is a 100 per cent consistent winner, only one polygon is drawn representing the course of the development of the population, averaged over all the replicates of the experiment. Whenever in the given conditions of temperature and humidity, the outcome of the contest varies from one replicate to the next, the corresponding figure gives two polygons, each averaging the consecutive censuses of replicates which end with the victory of one particular species.

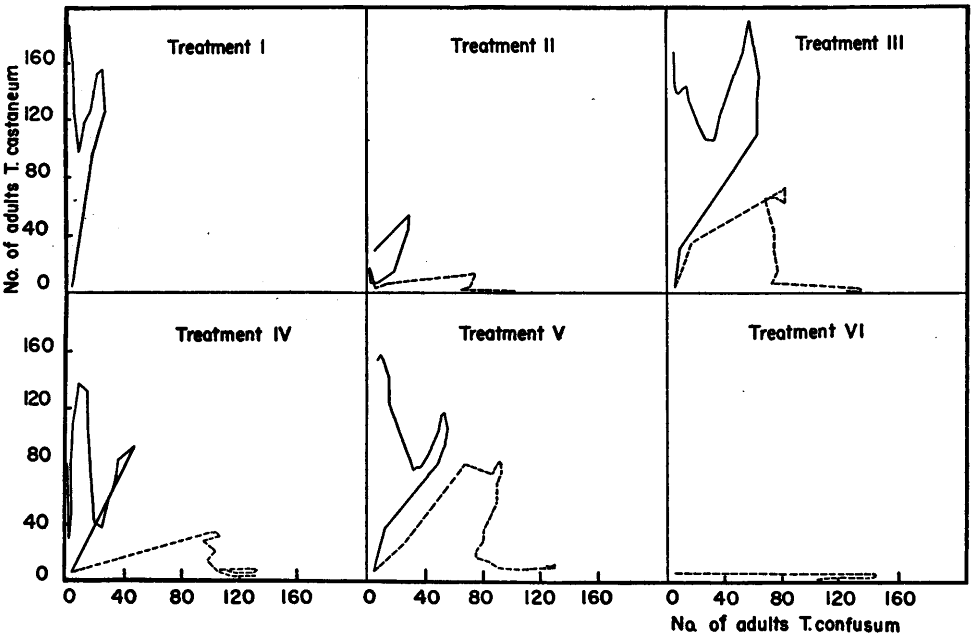


FIGURE 7

Average competition curves of *T. confusum* and *T. castaneum* under the six treatments.

The inspection of the six figures indicates a very close analogy with the prediction developed in connection with figure 5. It appears that, on a number of occasions, the first leg of the polygon is rather long and "overshoots" the band between the two lines of indifference. The subsequent censuses show a return to more moderate numbers, presumably within the band between the two lines of indifference, and then a gradual approach to one of the axes of coordinates. It is unfortunate that the information does not permit us to draw the lines of indifference. However, in each case, the position and the shape of the polygon suggest the position of these lines.

All the above discussion applies to the case in which, as in Park's experiments, one starts with equal numbers of adult individuals belonging to the two competing species. Suppose now that the design of the experiment is sharply modified to give the usually losing species a very considerable initial numerical advantage. More specifically, assume that one starts with a number of individuals of the first species many times greater than that of the second so that the point in figure 5 marked with the numeral 1 is shifted horizontally far to the right, beyond the two lines of indifference L_1 and L_2. In these circumstances, the change in the composition of the mixed population expected at the next generation will be characterized by an arrow directed approximately like that attached to point 5 in figure 5. In other words, it will be expected that in the next generation the number of adults of each species will be *less* than that in the original mixture. Since the starting number of the second species is relatively low, this would result in the danger of their dying out completely.

As a general conclusion, the proposed summary model of purely statistical interaction between the two species, appears to fit the observational results qualitatively. However, this does not mean that this, or a similar, model of statistical interaction will prove satisfactory when compared with the data quantitatively. In fact, it is not impossible that a closer study will reveal the necessity of adopting a hypothesis of some sort of biological interaction in order to be able to fit the data in all their details.

7. Studies of fecundity and cannibalism—a primitive model in the small

In the present section we describe a primitive attempt, and its failure, to obtain a satisfactory model in the small of one of the secondary phenomena of the class considered. This failure initiated a number of experiments and several theoretical studies directed towards a better understanding of the machinery behind the development of a population of beetles in simple conditions.

The fact that crowding adversely affects the growth of any population of organisms is very familiar. However, as far as the authors can see, the machinery of this process is not yet exactly understood. The phenomenon appears intelligible if the crowding is so intense that the particular organisms of the population lack some element necessary for their normal development, such as food, oxygen, etc. However, the apparent adverse effects of crowding are observable in conditions where there is no question of any sort of scarcity. Must one, then, assume the existence of some sort of biological factor (for example, "interference") which, for instance, causes a female beetle to lay fewer eggs when she is living in company with a few other beetles than if she lives with just one other beetle, a male?

The following experiments were performed with *Tribolium* by a number of searchers and always gave the same results. In a vial of fixed size one places a fixed amount of flour and a certain number n of pairs of beetles, as far as practicable of the same age. The experiment is replicated a reasonable number of times with the same value of n. After a suitable period of time, far too short for any of the eggs to hatch, the contents of the vials are examined and the eggs counted. The number of eggs recovered is divided by n so as to obtain the average number of eggs recovered per one female. Invariably the trials of this kind indicate that the average number of recovered eggs per female (net fecundity) is a decreasing function of n [31], [46], [47], [51], [52].

This is an interesting secondary phenomenon in the process of development of a population and its satisfactory explanation is an obvious prerequisite to the complete understanding of the primary phenomenon.

In order to explain the decrease in the net fecundity of *Tribolium* accompanying the increase in crowding, one is tempted to begin with the simplest possible hypotheses (1), (2) and (3) enumerated in the preceding section, supplemented by the following.

(4) To every female beetle alive at time $t_2 > t_1$, to every time interval (t_1, t_2) and to every integer $m \geqq 0$ there corresponds a probability $P_m(t_1, t_2)$ of laying exactly m eggs in the time interval (t_1, t_2), namely

$$P_1(t_1, t_2) = (t_2 - t_1)\lambda + o(t_2 - t_1) \tag{25}$$

and

$$P_m(t_1, t_2) = o(t_2 - t_1) \quad \text{for} \quad m > 1 \tag{26}$$

where $\lambda > 0$ is a constant characterizing the real fecundity of the beetle. This probability does not depend on the number of eggs laid before the moment t_1 nor on the times at which these eggs may have been laid.

If a vial contains n pairs of beetles and, if the value of the constant λ is the same for all the n females, then simple reasoning implies that the number X_m of eggs to be found in the vial after a fixed time T, is a Poisson variable with its expectation equal to

$$E(X_n|T) = \lambda \frac{1 - e^{-2n\mu T}}{2\mu} \tag{27}$$

where, as formerly, the symbol μ represents the measure of voracity of the beetles in the vial, supposed to be the same for all of them. Dividing the above quantity by the number n of females in the vial and by T we obtain the expectation, say $F(n)$, of the net fecundity per female per unit of time, computed on the assumption that there are n pairs of beetles in the vial,

$$F(n) = \lambda \frac{1 - e^{-2n\mu T}}{2n\mu T} . \tag{28}$$

It will be remembered that this formula was deduced on the assumption that, during time T, all the females lay their eggs in a random fashion but at a constant rate λ, and that the voracity, measured by the factor μ, remains unchanged. Yet, it is easy to see that the expected net fecundity $F(n)$ is a decreasing function of n. This is the consequence of the fact that the derivative

$$\frac{d}{dx} \frac{1 - e^{-x}}{x} = \frac{e^{-x}(1 + x) - 1}{x^2} \tag{29}$$

is always negative, because of the familiar inequality

$$e^x \geqq 1 + x . \tag{30}$$

By the same argument we find that the expected net fecundity per female per unit of time is a decreasing function of the time of observation T.

It will be seen that qualitatively the above consequences of the simple model in the small of statistical interaction between fecundity, cannibalism and crowding are consistent with the observation. However, as was pointed out at the conclusion of the preceding section, this does not necessarily mean that the same model will stand up to a closer quantitative comparison with the experimental results. In actual fact, a series of experiments performed by Dr. Earl R. Rich [31] provides data invalidating completely the model just presented. We reproduce in figure 8 some of his findings which are particularly relevant to the present discussion.

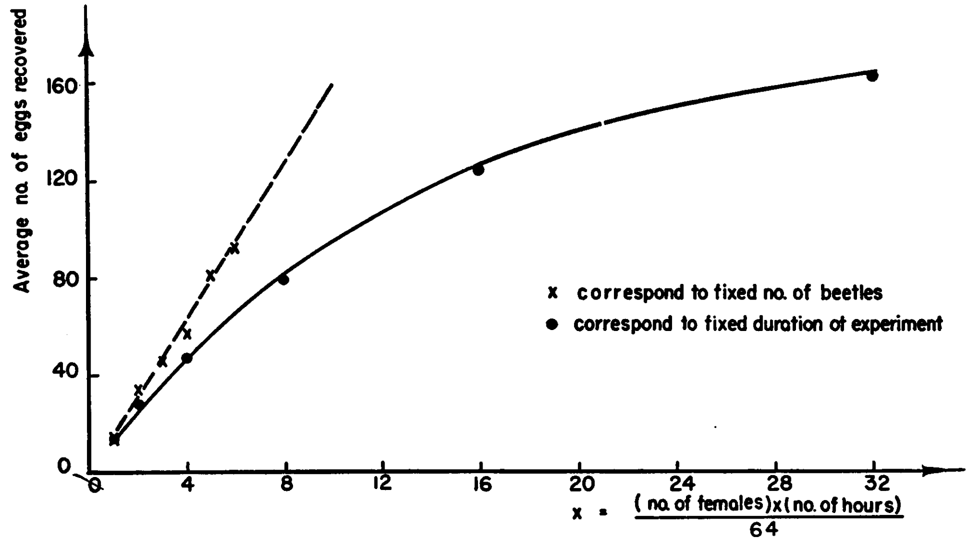


FIGURE 8

Dependence of net fecundity of *T. confusum* and duration of experiment IV on crowding (Rich's data).

According to formula (27), the expected number of eggs to be found after a period of time T in a vial containing $2n$ beetles depends, say, on the product of these two quantities $2nT = x$. It follows that, for example, 16 beetles during eight hours should produce essentially the same number of recoverable eggs as eight beetles during 16 hours, etc. Figure 8 based on Dr. Rich's results, illustrates the fact that the actual dependence of the expected number of recovered eggs on time and on the number of beetles is more complex.

The quantity measured on the horizontal axis in figure 8 is x expressed in conventional units equal to (8 beetles) × (8 hours). The quantity measured on the vertical axis is either the average number of eggs recovered by Dr. Rich in several replicates of this experiment or the expectation of this number obtained from formula (27). In particular, points marked by crosses correspond to Dr. Rich's observation in which the number of beetles was constantly equal to 8 and in which the increase in x was obtained by increasing the duration of the experiment, 8, 16, 24, 32, 40, and 48 hours. The sequence of these points was fitted by a continuous line corresponding to the equation (27) with $\lambda = 11.74$ and $\mu = 0.000375$. In evaluating these constants the unit of time was taken to be 24 hours.

The points in figure 8 marked by filled circles correspond to Dr. Rich's experiments in which the duration of the experiment was constantly the same, namely 8 hours, and the increase in the argument x was achieved by a corresponding increase in the number of beetles in the vial, 8, 16, 32, 64, 128 and 256. The line passing about these points corresponds to equation (27) with $\lambda = 10.16$ and $\mu = 0.0289$.

If the model corresponded to reality, then the sequence of the filled circles and the sequence of crosses would approximate the same curve corresponding to equation (27), and would deviate from it only by virtue of random variation. Contrary to this, the two sequences of experimental points, obtained from independent observations, are very regular but one is distinctly below the other. The inevitable conclusion is that the model considered in this section is distinctly too primitive to represent the mechanism of oviposition and cannibalism. There is an easy way to achieve a better agreement between the theory and observation. It consists in introducing into the model a hypothesis of biological interaction, to the effect that the fecundity of the beetles, and perhaps also their voracity, depend on the degree of crowding. However, before embarking on this path, the authors decided to examine other hypotheses involved in the model. These studies are still in progress. Their direction and some of the results are reported in the following section.

8. Current studies

The first of the hypotheses underlying the above primitive model that was subjected to detailed study was the hypothesis of the constant rate of oviposition denoted by λ. The process of aging of beetles must have some effect on fecundity and, probably, also on veracity. Accordingly, the original primitive model was modified by the substitution for the two constants λ and μ of unspecified functions $\lambda(t)$ and $\mu(t)$ of the age t of the beetles. Under this hypothesis, the number $X_n(T)$ of eggs recovered after the lapse of time T from a vial containing n pairs of beetles, is again a Poisson variable. However, its expectation is represented by a formula depending on the nature of $\lambda(t)$ and $\mu(t)$, substantially more complex than formula (27).

These results were further extended by Dr. C. L. Chiang who studied several interpolatory formulas which appeared likely to provide satisfactory approximations to the unknown function $\lambda(t)$. Dr. Chiang [53] has produced methods for the estimation of the parameters in these formulas and applied his results to the experimental data obtained by Dr. C. Kollros. These data refer to the fecundity of "uncrowded" beetles, one pair of *T. castaneum* per 4 gms. of medium. The principal results of these studies are: (i) the particular females vary substantially in their fecundity; (ii) contrary to expectation, the function $\lambda(t)$, which may be termed age-specific fecundity, appears to have not one but possibly three consecutive maxima. Figure 9 gives a graph of the interpolatory formula fitted by Dr. Chiang and also a series of empirical points, each representing an average of several replicates of Dr. Kollros' [54] experiments. It will be seen that, while the age-specific fecundity varies substantially over the lifetime of the female, periods of several days' duration can be selected over which this variation is negligible. Therefore, it may be expected that the outcome of Dr. Rich's experiment was not affected by the change in the fecundity of beetles that could be ascribed to this aging.

The other hypotheses in the primitive model that are being subjected to a closer study are those relating to the machinery of cannibalism. It will be seen that the only realistic moment in the actual machinery that these hypotheses reflect is that cannibalism develops in time, along with oviposition, and that the only eggs that may be cannibalized at a given time are those that have been already laid. After taking into account this obvious fact, the development of the model followed the line of least resistance leading to easily obtainable formulas. On the other hand, it is obvious that the chances of finding and eating an egg must depend on the pattern of egg deposition and on the manner in which the beetles search for eggs. Also, it is obvious that the process of searching for eggs must involve some elements of randomness. Thus, in order to be able to formulate more realistic hypotheses regarding cannibalism, the authors were led to the study of random walks of beetles. In order to provide the necessary data, two substantial experiments were set up. Details of the results will be published elsewhere.

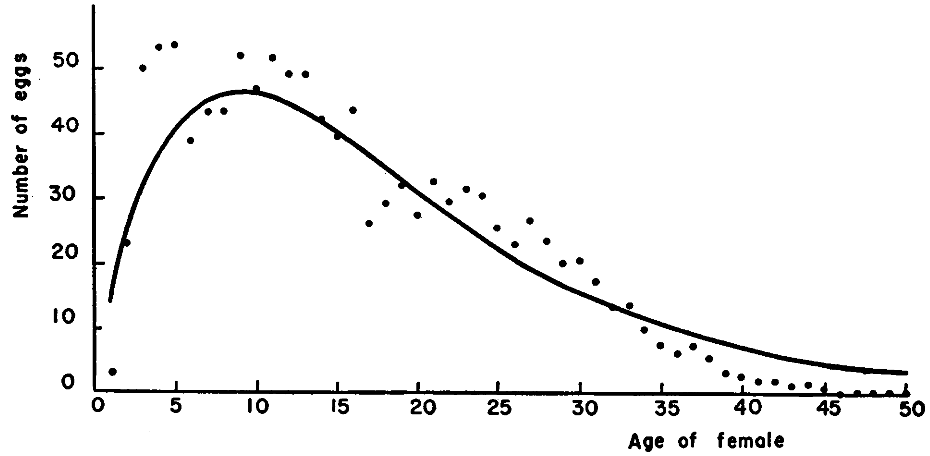


FIGURE 9

Age specific fecundity of T. Dots represent number of eggs per day observed by Kollros. Continuous curve, fitted by Chiang, corresponds to equation

$$\beta(t) = (a + bt)e^{-ct}.$$

Deviations of empirical points from the line appear real, not effects of random variation.

One of the experiments is intended to provide direct information on the characteristics of the movements of the male and the female beetles. For this purpose, pairs of beetles were marked with minute lead fragments and placed in containers filled with flour. Next, series of X-ray photographs were taken from each container at time intervals of 15 seconds, 45 seconds, then again 15 seconds, etc. It is planned to use these photographs for the study of the joint distribution of velocities and of displacements of the beetles.

The second experiment was meant to provide information about the limiting distribution of living and dead adult beetles of the two sexes, and about the distribution of larvae and pupae, attainable after a considerable time during which the beetles are allowed to travel.

A container was filled with fresh flour occupying the volume of a cube 10″ × 10″ × 10″. On the surface of the flour a total of 2257 adult *T. confusum* beetles was placed with a 1 to 1 sex ratio. The container was kept for a month in a dark incubator maintaining approximately constant temperature of 29° C. and approximately constant humidity of 70 per cent. Also, in order to equalize the possible gradients of temperature within the incubator the container was periodically rotated. After four months, at which time the population totaled 73,009 individuals excluding eggs, the contents of the container were divided into one thousand cubes 1″ × 1″ × 1″ and the contents of each small cube were lifted separately and examined. In spite of all the care in performing this operation, weights of the material lifted from particular small cubes differed. These weights were recorded for each of the small cubes along with the numbers of the various forms of *Tribolium*. The numbers of the different forms were divided by the weight of the medium in each small cube and provided measures of the density of these forms per cube which were later associated with the position of each cube. Figure 10 illustrates the results obtained. It represents the plan of the second layer from the top of the experimental cube and

18.8 28.7	22.7 24.2	16.1 14.2	12.4 12.0	12.8 11.1	13.8 15.3	11.0 14.1	14.4 18.1	11.8 20.2	16.7 23.0
10.1 14.8	11.2 6.9	9.6 3.8	7.9 3.1	7.3 5.3	7.3 3.5	5.1 3.2	4.3 4.9	6.9 8.0	11.9 16.0
7.9 13.3	6.5 4.6	5.7 2.0	4.4 1.7	3.5 1.0	3.6 1.9	4.4 1.9	5.9 1.9	8.4 3.5	10.4 9.8
9.9 9.5	6.9 4.5	5.4 1.5	5.8 .7	3.2 1.3	2.9 1.3	3.1 .2	5.2 1.0	7.0 1.7	8.7 7.7
10.9 12.5	6.6 4.6	3.0 4.6	2.6 2.2	4.0 2.0	4.2 2.5	3.9 3.9	3.5 1.6	5.8 2.2	17.8 12.2
6.0 8.0	7.8 4.5	7.2 2.4	2.4 1.8	1.0 1.3	3.5 3.3	4.0 1.8	4.0 2.4	6.2 3.5	16.5 19.4
10.5 10.6	6.5 3.5	1.2 5.1	5.7 2.0	4.7 .4	4.2 1.9	5.4 2.3	3.7 .9	9.7 3.0	14.2 12.2
14.9 15.8	10.8 5.9	4.9 2.8	3.9 2.7	4.0 .8	3.5 1.4	5.8 2.8	4.3 1.7	7.3 3.8	13.3 11.8
18.3 26.6	10.4 8.9	8.5 3.4	5.3 4.6	5.6 2.7	4.8 3.5	6.4 2.5	8.3 2.4	8.2 4.9	12.1 18.6
19.1 35.2	12.6 14.1	15.8 17.0	14.7 17.2	12.8 21.8	11.4 13.9	12.9 14.9	12.3 12.2	11.5 14.1	17.1 34.5

FIGURE 10

Plan of layer II of big cube. Upper figure in each cell = density of females. Lower figure = density of males.

the distribution of densities of adult males and females within the 100 constituent small cubes. The general character of this distribution in other layers is very similar. However, the average density of beetles shows a marked decrease from the top of the container downwards.

Of the two numbers in each cell of figure 10, the upper represents the density of females and the lower the density of males. It will be seen that both densities exhibit a marked regularity. The greatest densities are observed in the four corner cells. Also, there is a general increase in density from the center of the layer towards the walls of the container. Finally, it will be noted that these general tendencies for males and for females differ substantially in their intensity. The unavoidable conclusion is that, while the random walks of the male and of the female beetles are likely to follow the same general law, some parameters intervening in this law must have different values characterizing the two sexes.

A number of models of random walks was tried in an effort to obtain a limiting distribution approximating the above distribution obtained empirically. Thus far none of these trials was successful. However, it may be of interest to mention some of the results.

One of the first hypotheses considered was that suggested by David Kendall [54], for the random walk of another organism, namely, that this walk may be comparable to Brownian motion of particles. This hypothesis was abandoned by the authors for the reason that the "velocity" of Brownian motion is infinite, while the quantities μ, used to characterize the rate of searching for eggs per unit of time, are certainly finite and rather small. However, the scheme of independent increment appeared appealing and the second model tried was based on the assumption that either the velocity of beetles or the acceleration is a stochastic process with independent increments. These hypotheses were also abandoned because of one unexpected consequence they imply. This is that the value of a coordinate at a fixed time of a beetle in a random walk of this character must be very highly correlated with this beetle's corresponding velocity component at the same moment, something which is unacceptable intuitively and is contradicted by the observation based on the X-ray photographs described above.

The most promising approach to the problem of a limiting distribution approximating the empirical one exhibited in figure 10 was uncovered by Dr. Bernard Sherman. This approach consists in the application of the general results on Markoff processes described by Feller [50] to some simple schemes of random walk on a square lattice in a plane, with inelastic boundaries. However, the analysis of two such models led Dr. Sherman to the conclusion that the limiting distribution of probabilities is characterized by exactly three nonnegative numbers: a = probability of finding the beetle at any specified interior point of the lattice, b = probability of finding the beetle at any specified point of the boundary, other than a corner, and c = probability of finding the beetle at any specified corner of the lattice. Thus, with appropriate supplementary conditions, this limiting distribution can represent accumulations in the corners and somewhat lesser accumulations of beetles at other points of the boundary. In this the theoretical limiting distribution resembles the empirical one in figure 10. However, thus far no system of assumptions has been discovered implying anything like the gradual density decrease in all directions from each of the four corners of the container.

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