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Beetles, Competition, and Populations

An intricate ecological phenomenon is brought into the laboratory and studied as an experimental model.

Thomas Park

Let us begin with two seemingly unrelated words: *beetles* and *competition*. We identify competition as a widespread biological phenomenon and assume (for present purposes at least) that it interests us. We view the beetles as an instrument: an organic machine which, at our bidding, can be set in motion and instructed to yield relevant information. If the machine can be properly managed, and if it is one appropriate to the problem, we are able to increase our knowledge of the phenomenon. Unfortunately, however, this does not necessarily mean that the concept is thereby clarified. This could happen of course. But, alternatively, the problem as now enlarged could emerge as being more complicated—that is to say, broader and deeper than first imagined. And the machine itself could prove to be more intricate, even recalcitrant. Obviously there exists an intimate marriage between the machine, its operator, and the phenomenon. Ideally, this marriage is practical, intellectual, and esthetic: practical in that it often, though not immediately, contributes to human welfare; intellectual in that it involves abstract reasoning and empirical observation; esthetic in that it has, of itself, an intrinsic beauty. Perhaps these rather pretentious reflections seem far removed from the original words—beetles and competition. But I do not think this is the case.

We develop the story further. First, I offer some general remarks about competition—the phenomenon. Then, I say something about the beetles—the organic machine. Finally, I attempt to put the two together in a certain way—to pry, discreetly I trust, into the intimacy of their marriage (*1*).

Competition in the Abstract

Biological competition has been the subject of controversy and debate among those who have given it serious study (*2*). Considerable disagreement exists about its essential character and its significance. Such difficult questions as these inevitably arise: How can competition be formally defined? What are its component elements? How can its presence in a natural ecological situation be detected—that is, what constitutes adequate proof? When it does operate, what is the consequence of this for the competitors themselves? Is it a pervasive process, one always effectively in command, or rather, is it a safety valve, something called into account only after a certain threshold is reached? This is not the place to deal systematically with these matters, important as they are. That would be inappropriate and, I fear, tiresome. It is necessary, however, to establish a point which bears on later discussion.

It is often held that competition is mediated by two component, but different, processes. The first is called "exploitation"; the second, "interference." Exploitation operates when the organisms draw upon a particular resource (food, say) which is present in limited supply. The more limited this resource, and the larger the population draining it, the greater is the intensity of competition. Interference operates when interactions between organisms affect their reproduction or survival. For example, imagine two populations one of which is small and the other crowded. Assume further that more food is available for both populations than can be used (exploited). The small group readily obtains adequate nourishment but the crowded group does not, for the reason that its members so disturb each other that the *opportunity* to feed is restricted. If this causes a decrease in birth rate, or an increase in death rate, interference can be said to be functioning.

These points are shown schematically in Fig. 1. We see there four squares, each representing a physical habitat. The habitat is occupied by the populations of two species. We denote these as *X* (the closed circle) and *Y* (the broken circle). *R-1* and *R-2* refer to two different resources. The interference of *X* on *Y*, and of *Y* on *X* is indicated below each square as being absent (0) or present (+). We can now examine in the light of the preceding comments what should hold true when competition between *X* and *Y* is indeed a reality.

In situation I we note that although species *X* and *Y* are living together in space and in time they are actually exploiting quite different resources and are not interfering with each other's reproduction and survival. We therefore conclude, a priori, that the biological stage is arranged in such a way as to make it impossible for interspecies competition to exist. This is the null case. Situation II depicts the two species as

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The author is professor of zoology at the University of Chicago, Chicago, Ill. This is the text of his address as retiring president of the AAAS, delivered 28 December 1962 at the meeting in Philadelphia.

drawing upon different sources of capital but interfering with each other. Situation III is the opposite of situation II: here, *X* and *Y* are withdrawing their capital from a joint account but interference is zero. We conclude that competition is operating in both situations II and III, but for diverse reasons. In situation IV, *X* and *Y* are utilizing the same resource, but, since they are also engaged in interference, we deduce that competition, thus doubly assured, is intense. These arguments seem logical. Later we shall ask whether indeed they are biological.

Competition Experimentally Viewed

Let me be less formal, less academic. It is not difficult to imagine local populations of two species which share a common geography; which exploit, at least in part, certain of the same resources; and which interfere with each other's reproduction and survival in a manner that is neither haphazard nor frankly predatory. Under such conditions we infer that competition should be operating. But how can the inference be proved? Suppose we find it feasible to count both groups and thereby record the changes in their numbers generation after generation. Suppose, further, that there is no appreciable immigration and emigration. We graph the accumulated data (species *X* and species *Y* against time) and search for *pattern*.

To illustrate the difficulty of the problem, I have generated two artificial patterns, making use of a table of random numbers. These appear in Fig. 2 and are there referred to as case 1 and case 2, respectively. Despite the fact that, biologically speaking, the curves are quite fraudulent, they do bear a seductive resemblance to the behavior of real populations! In case 1 the only relation between the two "species" is purely coincidental, by definition. In case 2, on the other hand, matters have been so contrived that *X* is more abundant than *Y* for most of its recorded history, but there is an intermediate interval during which *Y* exceeds *X*.

Let us pursue the point. We now pretend that the graphs before us are actual rather than synthetic, and also that no information is available other than the census data themselves. Our question remains the same: Is competition operating in either instance? Regrettably, the question cannot be answered on the basis of the knowledge available. All we can do is to draw the following two, rather barren, conclusions:

1) Case 1 does not support an inference of competition. There is no consistent relation between the curves. However, the inference is *not disproved* because competition could be operating but its effect obscured by such extrinsic factors as, say, those variations of climate which characterize each year and which affect the reproduction and survival of both species.

2) Case 2 does support an inference of competition. *X*, characteristically the abundant species, declines significantly (though transiently) when *Y* increases markedly. However, the inference is *not proved* because the visual suggestion of competition could be illusory and the cause, again, could be extrinsic, such as, for example, a particular sequence of seasons more favorable for the increase of *Y* than of *X*.

But there is another point, essential for the argument, that emerges from our brief consideration of Fig. 2. It is this: the information contained therein is retrospective and descriptive rather than prospective and based on experimentation. The curves illustrate the abundance of *X* and *Y* through time. But conditions extraneous to the presumed competition were not controlled, and, as I have tried to show, these could have played a causative role. In addition, we have been able to record the history of only one population of each species; our experience is limited. Traditionally, ecological findings are based on the chronicle of events which have taken place in an environment unmolested by the observer and varying according to its own natural right. Such retrospective studies attempt to explain what has happened on the basis of a single case history, and the derived data are candidates for some form of correlation analysis. Although I am in no sense contemptuous of this method, I am persuaded that progress in an area so complex as population ecology will be greatly facilitated by increased experimentation in the field. There is nothing original in this view. Certain workers consistently find it rewarding to manipulate the natural conditions. But I urge that this approach should accelerate, gain wider adoption, and perfect its techniques. In principle, if not always in practice, the method is limited by neither the taxonomy nor the habitat of the organisms being studied. Parenthetically, I believe it can even contribute to the solution of such pressing problems as conservation and the social biology of man. When a prospective plan is used, the dividends are agreeable. Time is saved; more questions are asked; appropriate treatments are replicated by design; and the data lend themselves to powerful methods of analysis.

There is, however, a different way to study populations and to do so prospectively and experimentally. That is to move a field problem into the laboratory. To do this one must find an organism which is conceptually and technically adapted to investigation of the phenomenon under consideration. In other words, we strive to erect an indoor *model* of an outdoor experience. Such models, though not simple, are simplified; they enjoy a regimen of planned control; their intrinsic interactions are likely to be intensified. To this extent they are unrealistic. But they remain, nonetheless, quantitative *biological* systems, and their unrealistic aspects often prove to be a virtue rather than a vice. Let us explore this matter.

Beetles: The Experimental Material

About 2500 B.C., a Pharaoh died and was entombed. When the site was studied various curios were found, including an urn which contained milled grain. Within the grain were the corpses of small insects known commonly as "flour beetles" and technically as *Tribolium* (*3*). Thus this genus, at least so far as one of its 26 known species is concerned, was apparently preadapted to living in flour in early historical times. As everyone knows, such beetles are important pests of cereals; in fact, large bureaus exist which are zealously engaged in searching for effective ways to destroy them and limit their dispersal. As everyone does *not* know, however, the same creatures are elegantly suited for certain types of ecological and genetic research; in fact, a few small "bureaus" exist which, with equal zeal, are dedicated to the beetles' welfare and conservation. Why should this be so? I shall attempt a brief answer to the question by introducing you to the organism; to the "organic machine," as I referred to it earlier.

A note of history: To the best of my knowledge, the flour beetles were first used experimentally by W. P. Davey, who, in 1917, reported on the relation between x-irradiation and the life duration of the adult stage (*4*). It was R. N. Chapman, however, who studied *Tribolium* as populations; who recognized its potential for this sort of research. That was in 1928 (*5*). Since that time a handful of ecologists have continued, and expanded, this tradition. And only recently, I am happy to report, the geneticists have discovered that the beetles have advantages for their own work (*6*).

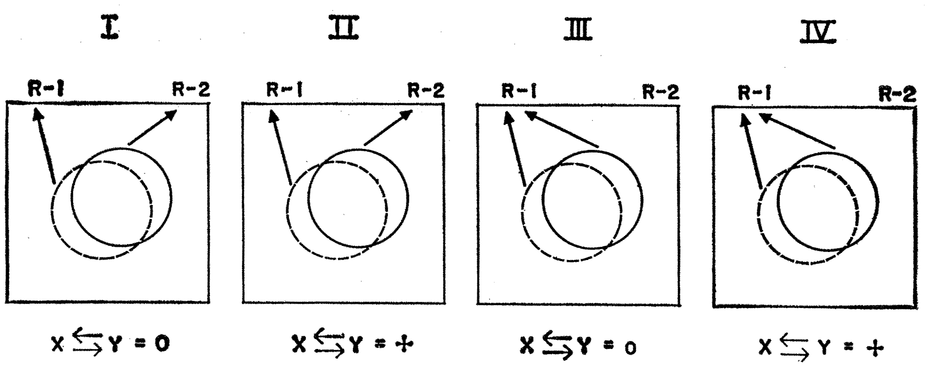

Fig. 1. Abstract representation of interactions that produce competition. *R-1* and *R-2*, two different resources; *X* and *Y*, the interference of one species population with the other (see text). In case I, competition is absent; in case II, competition exists, owing to the presence of interference (+); in case III, competition exists, owing to exploitation by both species (*X* and *Y*) of a shared resource; in case IV, competition is intense, owing to the fact that there is both exploitation and interference.

In order to perform efficiently, a laboratory population model must satisfy certain requirements. The major, technical ones are these. First, it must be possible to enumerate the population by accurate census. Second, it must be possible to reconstitute the population after each census without appreciable trauma to its membership. And third, it must be possible to control the environment in various ways and to manipulate it in various ways. The precise meaning of "environment" poses a problem of heroic magnitude, and I have no desire to involve you, or myself, in this polemic. But I do think that a certain clarification can be achieved by means of the following assertions. The environment can be viewed as being *spatial*; it has a geometric configuration. It can be viewed as being *climatic*; it has a definition, say, in terms of temperature, moisture, and light. It can be viewed as being *nutritive*; it is a reservoir of food, both in quality and quantity. It can be viewed as being *biotic*; it has a component evoked by interaction among living things. Finally, it must be viewed as being *temporal*; its other attributes are relentlessly influenced by the passage of time.

The technical utility of *Tribolium* stems from the simple natural-history fact that the beetles (and their immature stages) spend their life, and multiply, in finely milled flour. In other words, flour is the spatial, climatic, and nutritive environment neatly bundled into one convenient package. Space can be controlled merely by choosing a container of desired shape into which a known weight of flour is introduced. Climate can be controlled by maintaining unlighted cabinets at prescribed values of temperature and humidity and allowing the flour to come to equilibrium at these values. Food can be partially controlled by using flour which is always prepared in a certain way (quality) and apportioned in a certain amount (quantity). The biological and temporal aspects of the *Tribolium* environment are more effectively introduced somewhat later in this article.

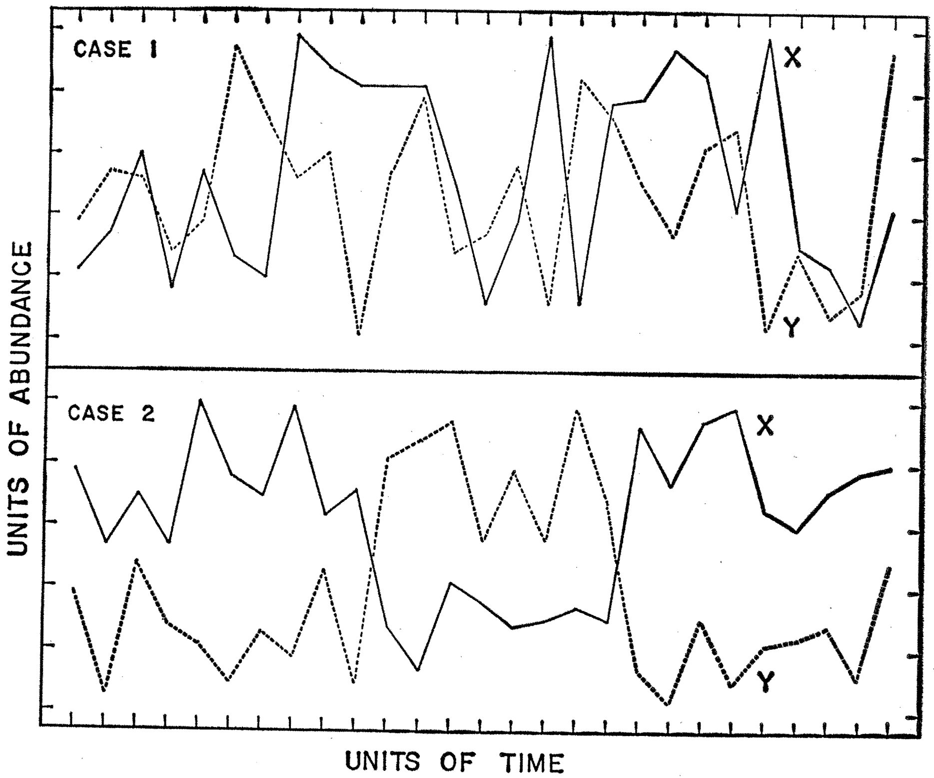

Fig. 2. Fabrication of two population case histories by means of a table of random numbers. There are two species, *X* and *Y*. In case 1 all assocation between the species is coincidental. In case 2, species *X* is permitted to exceed species *Y* except during the intermediate time intervals during which *Y* exceeds *X* (see text).

For every population study there is one type of basic datum. This is a record of the number (or weight) of organisms inhabiting a defined space at a particular time. But frequently such records are amazingly difficult to come by; in fact, it is sometimes possible to achieve nothing more than a shrewd guess. With the flour beetles, as I have suggested, we do not encounter this difficulty. A census can be readily taken, and though this is laborious and in itself unexciting, we can take pride in the accuracy of the results. Also, the beetles have given us no compelling reason to think that they are harmed by the procedure. I illustrate by describing a typical sort of census; one where a population is counted each 30 days (30 days is the approximate length of a generation at a temperature of 29°C). The method is diagrammed in Fig. 3. Populated flour is gently poured from its glass container through a series of silk sieves with meshes of different dimensions. This segregates the stages by size and accumulates for disposal the old, but now uninhabited, flour. After counting, and recording of the numbers, the total population is placed in another vial containing fresh flour and returned to the incubator, where, for an additional 30 days, the processes of death, survival, and reproduction go on.

A further point needs making. For studying interspecies competition in the laboratory, at least two distinct species are obviously required. And each of these must satisfy the requirements outlined earlier. The genus *Tribolium* provides such material; there are two satisfactory species. One goes by the quaint name of *Tribolium confusum,* while the other has been christened *Tribolium castaneum.* For convenience, I retain the notations used earlier and refer henceforth to the former as *X* and to the latter as *Y*. Both *X* and *Y* are husbanded in exactly the same way and censused in exactly the same way, and both dwell in flour. Thus, for any predetermined (prospective) set of climatic, spatial, and nutritive conditions, *X* can be studied as a single-species population; the same holds true for *Y*; and *X* plus *Y* can be combined as a competition model. The significance of this statement should be fully appreciated because, in many ways, it lies at the heart of our story. Its meaning is this. If we measure what *X* does and what *Y* does when both are *alone,* we thereby are able to detect and evaluate what is *new,* or competitive, when both are together. Extrinsic factors, being controlled, no longer mask the data. The intrinsic factors remain, but now they are under surveillance. They constitute the biological and temporal aspects of the environment. This is the intellectual advantage of the model—an advantage very difficult to achieve outside the laboratory. It is, in part, what was meant earlier by the comment that such models, though not simple, are simplified. Gratifying as all this is, however, it does entail an element of risk: the risk that the investigator may be hypnotized by the data as such, concern himself only with the model, and forget the general phenomenon. Since there is a reasonable chance of answering the questions asked, why not shed the burden of theory? That is to say, instead of speculating about such matters as exploitation and interference, why not claim (quite cogently) that competition has been invoked if the behavior of *X* and *Y* together differs demonstrably from the behavior of *X* and *Y* alone? This is indeed a comforting position when one is immersed in analysis of a particular investigation. But, even though I take it, I do not applaud it. It is purely an operational convenience which, in the long run, may restrict one's contemplation of the phenomenon as a whole. The model should be more than an edifice in its own right.

We return to Fig. 1, there to refresh our memory about situation IV. This is the case for which the deck is stacked in such a way as to maximize the intensity of competition. Both species are exploiting a common resource, and both are engaging in interference. We now transfer this situation to *Tribolium.* The abstraction can be put to empirical test. *X* and *Y* are obviously competing for food, and for space in which to live. They are also interfering with each other. Some types of interference have been experimentally studied. Among these may be mentioned the relation of crowding to egg production, to rate of development, and to adult longevity, and a special sort of behavior [which overlaps predation (*1*)] involving the cannibalism of eggs and pupae by larvae and adults. It is probable that still other patterns of interference are as yet undetected (*7*).

To recapitulate briefly, I have suggested that there exists in organic nature a phenomenon known as "competition." I have presented, in terse form, something about the difficulties that arise in its serious study. Finally, this led me from outdoors to indoors, to the introduction of a laboratory organism which has certain properties, both conceptual and technical, that can be adapted to investigation of the problem at hand. I now wish to summarize some results in order to illustrate what happens when the "machine" is put to work.

An Empirical Illustration

A number of reports dealing with *Tribolium* competition have been published, and others are being written (*8*). I select one which illustrates some of the matters discussed earlier—specifically, a study concerned with the relation of six different climates to the population performance of *X* alone, *Y* alone, and *X* interacting with *Y* (*9*). Climate, now under supervision, remains an extrinsic factor but one no longer capricious. The response of each of the two species to climate is a quantitative measure of *intra*species competition. The response of the two species in association measures whatever additional impact arises from *inter*species competition. Owing to the fact that the research is prospective, the treatments can be chosen in such a way as to favor the chance that the phenomenon will be illuminated. It is also mandatory to initiate, not one population per treatment, but just as many as manpower, stamina, and patience permit, in the context, of course, of the demands made by the experimental design. Let me comment on the last point. Somewhere there may lurk a person who holds the view that laboratory population studies (unlike their field counterparts) are easy and quickly consummated. The facts are just the opposite. Maintaining the laboratory and collecting the data is drudgery. I cite some statistics. During the next few paragraphs I summarize a certain investigation in an abbreviated way. In point of fact it required over 4 years to do nothing more than obtain the observations necessary for the analysis: 400 individual populations were sifted and examined every 30 days, and some 3 million beetles were counted. Basically, however, this is irrelevant and immaterial though, I hope, not incompetent. The *real* point is that the opportunity to work prospectively with such a machine as the *Tribolium* model creates, in itself, an obligation to operate that machine at high capacity. But I digress. Let us return to the issue at hand.

We establish six constant climates defined in terms of temperature and moisture and, for convenience, name them as follows: hot-moist, hot-arid, temperate-moist, temperate-arid, cool-moist, and cool-arid (*10*). Into each of the climates we introduce a set of control cultures (*X or Y*) and a set of experimental cultures (*X and Y*) (*11*). The procedures involving husbandry and census have already been described (Fig. 3).

In reporting the findings it is essential to gain some knowledge about the single-species populations before examining the mixed-species groups. A simplified summary appears in Table 1 in which the averaged total densities for both species are ranked within each column in relation to the climate the species inhabit. I draw three conclusions from Table 1: (i) both species persist successfully under the various climatic conditions (*12*); (ii) the *levels* of numerical abundance are affected by temperature and moisture; and (iii) *X*

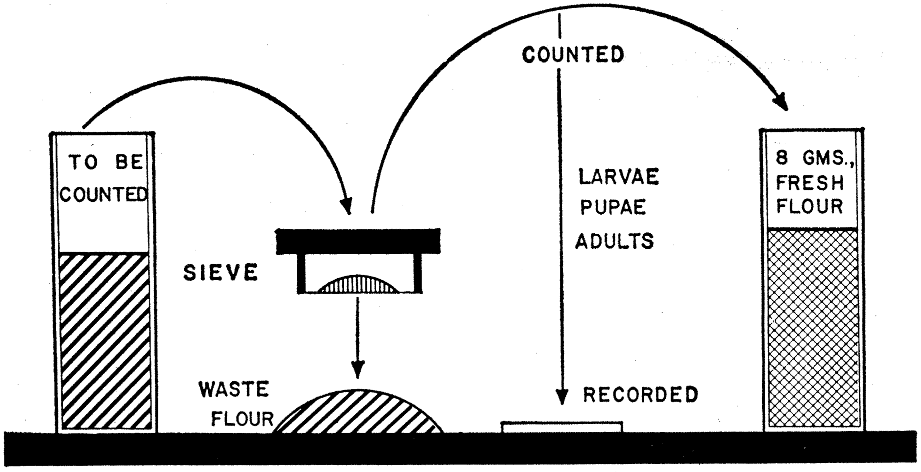

Fig. 3. Schematic diagram showing the technique of censusing a *Tribolium* population (census procedures at 30 days).

and Y do not respond in the same way to the environments in which they live. Thus, X is most productive in the hot-moist climate, while the density rank for Y in that climate is 3; X is least productive in the hot-arid climate, while the rank for Y is 5; and so on. In different words, the interaction between climate and *intra*species competition is reflected in the numbers observed.

When we examine what occurs when the two species are required to live together we are immediately confronted with a new, and qualitatively different, fact. It is this. One species is always eliminated and the other survives! Since it has been demonstrated that X and Y persist successfully when they are alone, it now follows that elimination of one species in the presence of the other is the result of sustained competition. But the matter is more complicated, more interesting. It can be pursued with the aid of Table 2. There, the six climates are listed in column 1; the single-species events are reviewed in column 2, but this time arrayed in a different way; and the competitive outcomes, in terms of percentage of contests won, are summarized in column 3.

Let us first consider column 3 of Table 2. We see there are two different patterns. One is unidirectional; the other, alternative. Let me explain. In the hot-moist climate Y always wins and X always loses. In the cool-arid climate X always wins and Y always loses. These end results are unidirectional. In the four other climates one species is always the *usual* winner ("usual" being defined as significantly greater than 50 percent), but for each case the other species wins *occasionally*. These results are alternative and can be thought of theoretically as being "stochastic." Thus, the consequences of competition are multifarious—multifarious in respect of climate, of species, and of frequency of success and failure.

Table 1. Average numerical abundance of single species X and Y ranked in relation to six different climates (rank 1, densest population).

Climate	Rank of X	Rank of Y
Hot-moist	1	3
Hot-arid	6	5
Temperate-moist	2	1
Temperate-arid	3	4
Cool-moist	4	2
Cool-arid	5	6

Now let us approach Table 2 in a different way. A glance down column 2 reveals that in one climate X is equal to Y, in three climates X exceeds Y, and in two climates Y exceeds X. If no other facts but these were available it might be amusing to attempt an extrapolation—to predict which species, in which climate, would survive in competition. A common-sense hypothesis immediately comes to mind: The species superior by itself should retain that superiority when with its rival. But, paradoxically, this prediction is rarely entirely fulfilled, as column 3 of Table 2 clearly shows. It is completely (see *12*) realized only in the cool-arid climate. It is usually, though not totally, fulfilled in hot-arid, temperate-moist, and temperate-arid climates. No rational guess can be made for the hot-moist climate, since there X is equal to Y. In the cool-moist climate it is actually the less successful single species, X, which usually wins the contest. I advance these points not to be mystical but rather to stress the fact that competition, even under supervision, is an extremely complex phenomenon. It is clear from what has just been said that *intra*species processes can be deeply modified by those new types of interference and exploitation which emerge as a consequence of togetherness. And it is becoming increasingly evident that such issues can be studied through a combined empirical and statistical approach, as P. H. Leslie has made abundantly clear (*13*). I think, also, that two points suggested at the beginning of this article here find illustration; the problem as now extended proves to be broader in scope than was at first imagined, and, in a sense, the machine has behaved in a more intricate fashion.

It is appropriate to illustrate one of the six competitive situations in a bit more detail. For this I choose the events seen in the cool-moist climate. This is a complicated case but an interesting one. The outcomes are alternative, but in large measure they fail to conform to an expectation based (a priori) on the performances of single-species populations. Let us examine Fig. 4. There, as smoothed curves, the numbers of adult beetles of species X (solid line) and species Y (broken line) are plotted against census time. The upper graph depicts the frequent outcome, or elimination of Y; the lower graph, the infrequent outcome, or elimination of X. In both instances there is an initial competitive period during which the two species are increasing. This is followed, again in both instances, by a period during which one species is progressively declining while the other is increasing. The increase eventually leads the successful species to a level of abundance which is statistically similar to that displayed by single-species populations of the

Table 2. The outcomes of competition between species X and Y contrasted with the individual performances of the two species in each of the six different climates.

Climate	Single species (numbers)	Mixed-species outcomes (% of contests won)
Hot-moist	$X=Y$	Y (100), X (0)
Hot-arid	$X>Y$	X (90), Y (10)
Temperate-moist	$Y>X$	Y (86), X (14)
Temperate-arid	$X>Y$	X (87), Y (13)
Cool-moist	$Y>X$	X (71), Y (29)
Cool-arid	$X>Y$	X (100), Y (0)

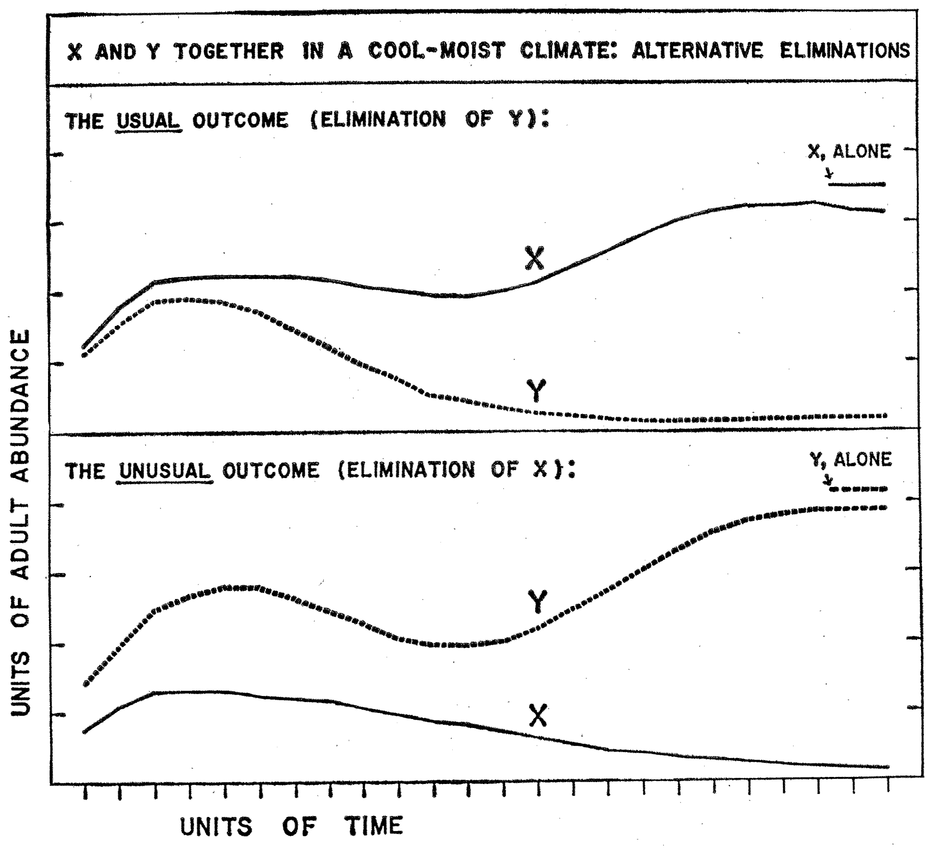

Fig. 4. Smoothed curves showing alternative outcomes for species *X* and *Y* when in competition in the cool-moist climate.

same age, suggesting that the travail of competition has not (in this case at least) left a permanent scar on the victor.

A new perspective is now possible. With the research finished, the curves of Fig. 4 obviously become retrospective, historical documents. But at this stage, I think, we enjoy an added confidence and an added understanding. We know that while climate has played an extrinsic role in determining the abundances of *X* and *Y* it has not caused population extinction. The latter results from interaction between the species—"the biotic and temporal aspects of the environment." We know, further, that the data have a certain generality. Instead of reporting an isolated circumstance they are based on the performance of 70 separate populations (20 of *X*; 20 of *Y*; 30 of $X + Y$). In short, we have advanced to a new status: a tentative inference of competition has become a fact, and the outcomes of the process have been established. There are of course many things we do not know. For example, why does *Y* sometimes eliminate *X*? Is the stringent competition here described a reality of outdoor nature or is it purely a consequence of keeping the species in confinement? There are other such questions, and all are difficult. But the mere phrasing of a proper question is a signpost toward its answer.

At this juncture the investigator plays a more active part. It becomes his responsibility to pose the next question, to run the machine differently. As has just been suggested, numerous opportunities confront him. He could proclaim an analytical interest in the competitive events that characterize, say, the cool-moist climate. Investigation in this direction leads to a study of mechanism; to an exploration of ecological and genetic causation. By increasing the understanding of how parts of the machine work together, the phenomenon is enlarged in *depth*. Alternatively, the investigator might proclaim a greater interest in *breadth*. He complicates the model in such a way as to make it biologically more realistic and by this means searches for further ramifications of the phenomenon. He might assert, for example, that climates do not really exist in six tidy packets of temperature and moisture but, rather, are characterized by their variability. Therefore, the promising thing to do is to program the research in such a way that climate becomes cyclic and what is measured is the added impact of *this* on *X* alone, *Y* alone, and *X* with *Y*. Or again, the investigator might proclaim that his work had yielded additional insight—insight about the phenomenon itself, about methods, about new items to observe and record. Therefore (he might argue) the time has come to forsake the model, move outdoors, and there start afresh. The course finally chosen is to a considerable extent subjective. Although the choice must be mediated by practical and intellectual values, nevertheless it does involve an element of taste. And it is here that an esthetic, an intuitive, quality insinuates itself into the domain which I have called "beetles, competition, and populations."

Conclusion

I have essentially finished my story. Its message has been a simple one. The population is difficult to study with rigor and even more difficult to understand. Populations can be investigated in a number of ways, several of which I have tried to suggest. Each way has its strengths and its limitations. I have concerned myself primarily with one method, the use of laboratory models. Because of conviction I have been careful neither to say nor to imply that this is the most rewarding approach. But it is the approach I know best, and one I find agreeable. There is, however, a new and exciting prospect that is emerging from the experimental study of populations—the prospect that mathematical theory may be able to attack even such intricate problems as competition. I have earlier pointed out how a certain generality is derived from a series of replicated experiments. But if mathematics can grasp data such as these, a greater abstract generality may ultimately result. There is a passage from A. N. Whitehead which precisely summarizes what I mean. In tracing the historical development of the science of electromagnetism Whitehead says (*14*): "This rapid sketch . . . illustrates how, by the gradual introduction of the relevant theoretic ideas, suggested by experiment and themselves suggesting fresh experiments, a whole mass of isolated and even trivial phenomena are welded together into one coherent science, in which the results of abstract mathematical deductions, starting from a few simple assumed laws, supply the explanation to the complex tangle of the course of events."

I am expected to close, I presume, with a remark about the "population explosion." I oblige. I am against it! I do not wish, however, to draw direct parallels between insects and men. But despite this reluctance, several facts have emerged from the study of beetles in their flour which seem to have general currency. One of these is that overexploitation and intense "interference" are perilous and that the peril increases as the population increases.

And there is another fact, one illustrated earlier: The largest population, if exposed to stress, does not necessarily enjoy the best prospect of survival. Man, as we all know and pontificate, has the intellectual talent and the technical skill to avoid such coleopterous hazards. In short, he has the capacity to manage his own population and (of equal importance) to conserve those myriad other populations on which he depends. But one thing is certain. If man does not manage *his* biology *it* will manage him. (*15, 16*).

References and Notes

1. There are other common ecological relations between species in addition to competition. These are the interaction between plant and herbivore, between predator and prey, and between parasite and host. The three differ from competition, however, in that they all share a built-in behavior such that one population is the attacked and the other is the attacker, with obvious consequences for both. Thus, horses "attack" grass; lynxes attack rabbits; tapeworms attack swine. Still other ecological relations are mutually beneficial, while at the pinnacle of specialization are those end products of convergent evolutions, populations which are socially structured.
2. Many of the points that I have raised here, and elsewhere, are of course not original with me. Several general references which pertain to various aspects of the problem of competition are as follows: G. F. Gause, *The Struggle for Existence* (Williams and Wilkins, Baltimore, 193 → A. C. Crombie, *J. Animal Ecol.* **16**, 44 (194 → E. Mayr, *Proc. Am. Phil. Soc.* **93**, 514 (1949); A. J. Nicholson, *Australian J. Zool.* **2**, 9 (1954); L. C. Birch, *Am. Naturalist* **91**, 5 (1957); C. Elton, *The Ecology of Invasions by Animals and Plants* (Methuen, London, 1958); M. S. Bartlett, *Stochastic Population Models* (Methuen, London, 1960); L. B. Slobodkin, *Growth and Regulation of Animal Populations* (Holt, Rinehart and Winston, New York, 1961).
3. A. Andres, *Bull. Roy. Soc. Entomol. Egypt* **24**, 74 (1931).
4. W. P. Davey, *J. Exptl. Zool.* **22**, 573 (1917).
5. R. N. Chapman, *Ecology* **9**, 111 (1928).
6. I. M. Lerner and F. K. Ho, *Am. Naturalist* **95**, 329 (1962).
7. Cannibalism, a special case of interference, has been recently studied by E. R. Rich [*Ecology* **37**, 109 (1956)], F. J. Sonleitner [*Physiol. Zool.* **34**, 233 (1961)], and J. L. Brereton [*Ecology* **43**, 63 (1962)].

→ T. Park, *Ecol. Monographs* **18**, 265 (1948); ———, D. B. Mertz, K. Petrusewicz, *Physiol. Zool.* **34**, 62 (1961).

9. T. Park, *Physiol. Zool.* **27**, 177 (1954); J. Neyman, T. Park, E. L. Scott, *Third Berkeley Symposium on Mathematical Statistics and Probability* (Univ. of California Press, Berkeley, 1956), vol. 4, p. 41.
10. The actual temperature and humidity values, in degrees centigrade and percentage of relative humidity, are as follows: 34°, 70 percent; 34°, 30 percent; 29°, 70 percent; 29°, 30 percent; 24°, 70 percent; and 24°, 30 percent.
11. All cultures were started with eight young adult beetles per vial; sex ratio, unity. Control cultures received four males and four females of species *X* or four males and four females of species *Y*. Experimental cultures received two males and two females each of species *X* and *Y*.
12. There is one exception to this statement. Single-species populations of *Y* eventually became extinct in the cool-arid climate (temperature, 24°C; humidity, 30 percent). However, they persisted for a longer time than they did when in competition with *X* in the same climate.
13. P. H. Leslie, *Biometrika* **49**, 1 (1962).
14. A. N. Whitehead, *An Introduction to Mathematics* (Holt, New York, 1911).
15. H. F. Dorn, *Science* **135**, 283 (1962).
16. I am deeply grateful to the following friends who read the manuscript and gave me the benefit of their advice: P. P. H. DeBruyn, P. H. Leslie, D. B. Mertz, and Philip Wylie. I am also greatly indebted to the late Sydney Hadfield for a color slide used in connection with the lecture.

Science for the Citizen: An Educational Problem

Academic scientists have a responsibility for educating the nonscientist in the nature of science.

James H. Mathewson

The importance of technical education has been the subject of much discussion in this country since the sputniks forced world-wide recognition of Russian scientific prowess. The Russians are attempting to fashion a social order founded on the methods and achievements of technology and to extend the power of this technocracy beyond their borders in order to compete with us politically, militarily, and economically. They possess a large and effective system of education which nourishes this effort.

We are naturally concerned about the state of our own educational system in the face of this challenge, but there has been a tendency to underrate what we have done and what we are trying to do and to suggest measures for improvement that are not suitable for a democratic, pluralistic nation. I think this is due to a failure to keep in mind our fundamental goals. We must state what we are trying to do in education before we start talking about how we are to do it.

In this article I point out some deficiencies in our methods for teaching science to nonscientists in colleges and universities, and some alternatives. But first I will attempt to outline the philosophy behind the criticism and the suggestions.

The Purpose of Education

The purpose of our schools is the development of free, capable, and responsible individuals aware of something beyond their desks or benches—within themselves, within their homes, within their society, and ultimately within the nature of the universe. In this we are not challenged, for although the Russians may produce men who are capable technicians, they are coerced and apathetic citizens.

Our system of education is predicated on the existence of freedom. There must be no pressures of arbitrary authority or special interest on teachers or students. The opportunity for education must be open to all, and each individual must be allowed to go as far as he is capable of going in a program of his own choosing. We cannot allocate individuals to various trades or

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The author is a research fellow in the department of chemistry at the University of California, Berkeley.