AN APPROACH TO A PROBLEM IN POPULATION DYNAMICS*

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This is the text of a lecture to a group of graduate students in zoology and entomology. It describes the first stage of an investigation of the population dynamics of Malacosoma pluviale (Dyar); what led to the problem; how the study was planned, and how it actually developed. Some examples show that previous experience may be used to advantage during the planning stage of an investigation, and that it also may help to exploit the first break-through that occurs. But another example shows that previous experience then may be a handicap, as it may keep one from seeing things as they really are. Thus, the second break-through in a new field is more likely to be accidental, no matter how deliberate it may seem in retrospect. In other words, research still progresses more erratically than our final reports suggest.

This is not the kind of paper one expects to find nowadays in a scientific journal. It is not a straightforward account of methods, results, and conclusions. Instead, it is a discursive personal account of the beginning of one investigation, and its attendant difficulties and mistakes. It was originally a lecture given to graduate students and faculty of the Departments of Entomology and Zoology of the University of Alberta in 1961. I chose this approach because I thought students should hear at first-hand how our investigations really develop chronologically, and not always in the logical way in which we report them. I wanted to show what prompted the investigation in the first place, and how its first important turning-points were reached.

The lecture was to be published, but has been withheld until now because some of its points depended on data presented in an accompanying lecture, and this supporting material had to be developed differently for publication. Now that the data are in print (Wellington 1964, 1965) there is no longer any restriction on the content of the original address. The factual material is drawn from my investigation of the population dynamics of the western tent caterpillar, *Malacosoma pluviale* (Dyar).

Most research papers show investigators moving in such straight lines that one feels they often must have known their conclusions before they obtained their results! It is unfortunate that published reports so consistently give this impression. They do so, of course, because space limitations in journals permit authors to describe only the ideal routes to discovery. The truly erratic paths that lead there, or the first faint sign-posts that indicate the most likely route are almost never described. As the limitations imposed here are not so severe, I can tell you not only about my destination, but also something of my reasons for going and my ways of travelling there. There must be some sort of outline to which we can refer, however, so let us see how a straightforward description of the early work might be summarized. . . .

In 1955, an outbreak of the western tent caterpillar was nearing its peak in the Saanich Peninsula of southeastern Vancouver Island. Because it offered an opportunity to study the effects of behavioral and climatic variations on the insect's population dynamics, I collected some eggs from the outbreak for experimental purposes, and also mapped its boundaries so that I could follow later changes in its extent.

In 1956, when the eggs hatched, I subjected the emerging larvae to a very simple activity test that exploited their response to light. This test revealed several types of larvae that differed in their ability to perform directed movements when they were separated from their fellows. Some were well-directed and active, others were disoriented and less active, and some were so sluggish that they scarcely moved. Controlled rearings showed that these differences were persistent, and that they also affected individual development and survival, because the various types of larvae differed in their ability to find and utilize food.

Artificial colonies composed of varying proportions of active and sluggish larvae were established, and their habits were compared with those of natural colonies in the field. These comparisons led to the identification of different types of natural colonies, and this discovery in turn enabled me to find areas where either active or sluggish colonies predominated. Once these areas were located, working hypotheses could be developed to account for their existence and predict the ultimate fate of the populations within them.

The first results suggested that behavioral differences may have a greater effect on an animal's population dynamics than theorists hitherto have supposed. But to establish this point it was necessary to subject the deductions arising from this thesis to repeated tests. Such testing has been the primary objective of the study since 1957 and, to date, accumulated observations tend to support the thesis in a most consistent way. For example, active individuals predominate in new infestations, but the sluggish component of the population increases as infestations age. Ultimately, most members of one generation are so sluggish that they cannot survive. Consequently, numbers within infestations so affected are drastically reduced.

Although very condensed and incomplete, this summary is sufficient to provide us with a framework for future reference (see also Wellington 1957, 1960). But why should anyone want to study the effects of individual differences in behavior or activity on a whole population? And if they must, why use the western tent caterpillar instead of some other animal? Furthermore, what led to the rather unusual method of separating the different types of larvae at the beginning of the investigation? And finally, though the summary seems tidy enough, was the progress of the work really so direct? Or was it sometimes saved accidentally from ineffectual circling? In the remainder of this lecture, I will try to answer these questions.

To answer the first three I must go back several years before 1955. Those of you who read population literature know only too well the continuing debates among the theorists. For those who are less familiar with this literature, I can summarize its central theme in the following way. Many animals are alternately scarce and plentiful. Their numbers

increase tremendously for a few generations, then decrease again. A major problem for economic zoologists is to find out what prevents their indefinite increase; and bad weather, exhaustion of food supplies, or overwhelming attacks by enemies are often given as reasons why populations decrease. The situation is not so simple, however, because the numbers of animals may continue to decline while the weather is favorable, and while food is abundant and enemies are scarce (Chitty 1960).

Although population theorists often disagree, such conflict would be welcome if it included suggestions for *experiments* designed to *disprove* hypotheses. More often than not, however, it involves only comparisons of all-embracing theories. At least this is how it seems to field ecologists, who also find a disturbing gap between what the major theories say should happen in the field, and what actually happens there. Many investigators therefore have been dissatisfied with population theory for a long time.

Before 1952, I was too preoccupied with studies of the effects of weather on the behavior of insects to be concerned with the theory and practice of population ecology. One cannot study the effects of weather on insects for long, however, without being drawn into some of the population controversies. But when I finally began to consider the various arguments, I found I was less concerned with some of their more evident misinterpretations of weather processes than I was with the way in which they neglected the behavior of animals.

My own experience made me notice an operational weakness in most studies of population dynamics. In many of these studies there was a tendency to concentrate on the developmental and reproductive processes of the animals, and on measurements of their mortality or survival, to the virtual exclusion of their behavior and activity. But this approach overlooked the stubborn fact that an animal that does not behave properly, or that does not maintain a certain level of activity at critical periods in its life, simply does not survive, let alone develop and reproduce.

The more I thought along these lines, the more I felt that the right kind of observation would show that widespread neglect of the influence of individual behavior on survival was actually obstructing the development of population theory. And this feeling was not just a product of the scientific chauvinism that might be expected from my studies of behavior; it arose from the observation that some of the major theories could not really be falsified in their existing form (c.f. Platt, 1964). This was my main reason for wanting to study the effects of the activity and behavior of individuals on the fate of a whole population. But I had to find an insect that would be suitable for such a study.

I had one hint from previous work that *Malacosoma* spp. might be suitable. In 1948, C.R. Sullivan and I had studied the light reactions of three species of *Malacosoma* that were prevalent near Sault Ste. Marie, Ontario. We were interested in the changes in response that might take place at high temperatures. And we had been following the usual procedure; scattering larvae at random on the platform of a choice chamber that had illuminated and darkened sides. The insects were expected to

take up positions dictated by their initial response to light at room temperature, then move to different locations if their response changed when the temperature was raised.

We had done virtually the same thing with other kinds of insects many times before. But when we used newly-emerged first-instar larvae of *Malacosoma* only a few acted in the expected way. The majority never moved after they were dropped on the platform. Consequently, we could not continue the experiment, because we could not tell how they reacted to light.

To solve this problem, we put the larvae back on their egg mass, so that they would be in a more natural situation. In effect, we made the egg mass the dark-light alternative, with its top illuminated and its bottom shaded. When all the larvae were allowed to remain together on their eggs in this way, they moved about very easily. And since this solved the technical problem, we proceeded with the investigation (Sullivan and Wellington 1953).

I wondered afterwards, however, why most members of these young colonies could perform directed movements while they were touching one another, but not while they were isolated. And if most of them were so dependent, why were a few so independent that they could perform directed movements while they were alone? I had to file this puzzle for future reference, however, because we had used all the available larvae. And eventually, of course, I stopped thinking about it.

But I remembered it again in 1952, when I began to think about the possible effects of individual behavior on a population. Here, apparently, was a group of insects that varied in activity and behavior as soon as they hatched. Besides, all the members of the genus also experienced great and comparatively regular changes in numbers. And some species made conspicuous tents, so that they could still be found without much difficulty when they were scarce. *Malacosoma* spp. thus had much to offer as experimental animals.

It was no help to realize this in 1952, however, because the tent-forming species were too scarce to provide enough material for testing. But when I saw the outbreak of *M. pluviale* on the Saanich Peninsula in 1955, I was again reminded of my earlier intentions, and pleased to see a good supply of one of the species that had provided the germ of the idea. And that is how *M. pluviale* became the experimental animal in the study.

It is worth noting that at this stage I had very little foundation on which to build a work plan. I knew nothing of the apparent difference in activity that I have just described, except that it existed. I did not know whether it was simply an intrinsic part of each individual's make-up, varying from time to time as the animal passed through different physiological states, or whether it was a real and persistent difference among individual *Malacosoma* larvae, stable enough to be exploited in the type of study I had in mind. Since it would not take long to find out which kind of variability was involved, however, I decided to plan the forthcoming investigation on the assumption that the difference would prove to be persistent.

The decision to plan the investigation in this way did not depend entirely on an act of faith. I had recently observed peculiarities in the

behavior of some arctiid larvae which suggested that such individual differences might in fact be stable. Also, as I came to realize later, my various lines of thought had been channeled during a brief conversation with Dennis Chitty just before I saw the tent caterpillars on the Saanich Peninsula. Thus my ideas concerning individual behavior were resting comfortably within a larger framework. And larger frameworks are always reassuring, even when one is scarcely aware of them.

During our conversation, Chitty and I discovered we were both dissatisfied with current population theories, and disturbed by the tendency of ecologists to treat the populations with which they worked as though they were monolithic structures, instead of collections of individuals. But Chitty also was circling an idea he has since stated more explicitly; namely, that the composition of a population might change with changing density, and that this qualitative change might have important effects on subsequent densities (Chitty 1960). Looking back, I do not believe I had carried my ideas about the effects of individual behavioral differences on populations quite so far (although my ready response to Chitty's well-nigh subliminal prompting showed me later that I had obviously been ready to do so). A few months afterwards, however, all that was clear to me at the beginning of my own study was that I not only had to determine how any variations in behavior might affect the survival of individuals within a population; I also had to consider these individual differences in terms of the changes in population quality with which they might be associated. Still later, when I had some results to interpret, I suddenly realized that my final plan of attack had been decided, virtually at the last minute, by that conversation with Chitty: a conversation, incidentally, that I had "forgotten" in the enthusiasm engendered by finding the *Malacosoma* outbreak and planning my investigation.

The first step in that investigation was to ensure that the differences observed in 1948 were truly persistent between individuals, not just internal changes within any individual at different times of the day or between successive days. If the former situation obtained, many things followed directly. Otherwise, I scarcely had a problem of the sort I had imagined. To establish the facts, repeated tests of identified individuals were required. And I needed a very simple and rapid screening method that would allow me to handle large quantities of material; e.g., perhaps more than 15,000 larvae per generation. It seemed best to exploit the difference in activity noted during 1948, as it appeared to be present as soon as eclosion took place. This, then, was one reason for using the laboratory test employed at the beginning of the investigation. But there was another reason that requires further explanation.

Some aspects of reality are unusual enough to seem unacceptable or even unbelievable when we first encounter them. In these days of team research and elaborate equipment, we tend to forget that explication of these unusual and often complex aspects of reality does not always require a complicated attack. In fact, some of our more mechanized attacks only obscure reality, or the approaches to it. And obscuring the path to an incredible result does not often encourage others to verify or disprove it.

A good example of what I mean may be found in Karl von Frisch's work on dancing bees (1950). Some of those early results and conclusions were quite unbelievable, but the experiments had a truly beautiful simplicity. Without such simplicity, other scientists might still be questioning von Frisch's conclusions. Because of it, they have been busily extending his results; though, unfortunately, not always with such elegant methods. Present-day biologists have much to learn from Professor von Frisch's approach to problems, therefore, and can profit from it in whatever field they intend to explore.

I was prompted by this line of thought to devise a very simple test for my own purposes. As each egg mass hatched at room temperature, I took its newly-emerged larvae and distributed them in a long line parallel to a fluorescent lamp, separating the individuals so that they had to move more than their own body length before they could touch any of their fellows. The reasoning was that any individual capable of independent, directed movement should proceed directly toward the light, whereas the others should stay where they were, or not move very far in any direction. This should separate any colony into at least two components. And the stability of each of these components then could be assessed by further testing.

The test worked very well. It was in fact my first breakthrough, because without such an easy, rapid, and definite means of identification of persistent differences among individuals, there would have been little time to do anything else. Because of the test and its results, however, the first part of the study opened automatically into a series of sub-projects that virtually had to develop along certain lines, often with results that were quite predictable, because they were the logical outcome of the existence of the behavioral differences.

Consider the results of the rearing experiments, for example. Larvae that differ in their ability to perform directed movements must behave in certain predictable ways when they are gathered into groups and placed near food. Very sluggish larvae should be incapable of fending for themselves, no matter how many are grouped together. And this proved true. Very sluggish larvae had to be placed on their food because they were incapable of locating it when there was no active individual to guide them, even when the food was only a few mm. away. Without proper care, therefore, they starved. And proper care included frequent inspections to ensure that they had not fallen from the food, because they could not return to it unaided.

More active, but still disoriented larvae proved relatively easy to handle, as long as they were kept in sufficiently large groups. Then they spun sufficient silk to be protected from desiccation, and they eventually found food by a sort of group "amoeboid" flow. Thus they fed and developed, though with some delay.

In contrast, the independent larvae were more difficult to handle under artificial conditions. They were too independent in the rearing jars; a predictable result of their ability to orient and

travel while isolated. Although each could find food very quickly, individuals tended to remain scattered for hours instead of clustering together occasionally. Therefore they had few opportunities to form the common mat of silk that would protect them from desiccation, so that they often died when only small numbers were kept together in the jars. Increasing the number of larvae per jar, however, solved this problem.

As development proceeded, it was clear that the most active larvae fed more and developed most quickly, whereas the most sluggish, if they lived at all, fed least and grew most slowly. There was no evidence within the generation that disease or any malfunction not attributable to the basic differences was at the root of such variation. There was plenty of evidence, however, that eggs laid by some females yielded colonies that had a high proportion of *sluggish* larvae, whereas eggs from other females yielded colonies that had a much greater proportion of *active* larvae.

Many other differences in behavior and activity were revealed during these studies, which opened endless avenues for further physiological research. But I must confine my remarks here to the development of the population studies. The foregoing descriptions were necessary to emphasize that there were some very marked differences in development and survival associated with the differences in activity and behavior, even though the latter were first revealed as an apparently trivial response.

As the rearing experiments with pure groups progressed satisfactorily, I began to make up artificial colonies differing in the proportions of the types of individuals they contained. These were studied in the laboratory and in the field to determine what differences in growth or habits they might have. Those which contained numerous well-directed larvae were active. They formed several tents in rapid succession, spacing them widely over the available foliage, and vacating each in turn before they exhausted the food nearby.

In contrast, colonies that contained a high proportion of sluggish individuals were very inactive. Such a colony seldom made more than one tent, and the larvae spent much time clustered on it, because there were not enough active individuals present to disturb and scatter the other larvae resting in the cluster. The larvae enlarged the tent and occasionally fed out from it for short distances, but even when they had exhausted nearby food they seldom moved on to spin another tent, though ample food was available only a short distance away. Consequently, the members of truly sluggish colonies usually starved. If they were saved from this fate by unusually abundant food right at hand, they were still prey to disease. (They were more exposed to infection than members of active colonies, because they often touched the remains of diseased larvae during their prolonged clustering periods.) Very sluggish colonies, therefore, soon were lost to the population by one or other of these means.

When I finally obtained adults from the different types of larvae, I found that activity differences were still recognizable, and that their classification could depend once more on a very simple

test. Active adults left in the jars in which they emerged literally battered themselves to pieces in one or two days. From this extreme there ranged a graded scale of decreasing damage to the other extreme: the perfect appearance of sluggish adults that remained unmarked until they died. They never moved after their wings expanded.

All the findings described above came from straightforward exploitation of the logical consequences of the original differences observed among emerging larvae. They were necessary steps in the study, but most of them could not immediately add to its further development. As an isolated group of facts they offered no direct entry into the next stage: the study of the natural population. In fact, while all these sub-projects were in progress, I had been trying to find a way to distinguish the different types of natural colonies in the field without having to classify every larva within them. Without a simple and rapid method of classifying the natural colonies, I could not progress with the field studies.

The artificial colonies finally provided the solution to this survey problem. For not only did the active colonies among them make more tents than the sluggish colonies; they also made tents of a different shape. The "active" tent was longer and thinner -- in most instances very obviously club-shaped -- whereas tents made by less active colonies were shorter and squatter; in extreme instances, definitely pyramidal.

Here I had the potentially perfect sorting method to bring order out of the apparent chaos of the peak population of 1956, provided that natural colonies behaved as the artificial ones had. If they did, I could close the gap between laboratory and field studies by using differences in tent shape as a simple but reliable survey tool to classify every colony I examined. With it, I should be able to see whether there were areas where one type of colony predominated. In addition, I should be able to accumulate statistics on differences in the sizes of feeding areas, larval numbers, etc., among colonies. I also should be able to identify colonies that had changed their characteristics during development after losing one or other of their constituent groups, because these changes should be revealed by differences between their previous and current tests.

With so many potential benefits due, I was almost afraid to examine natural colonies again in case the difference did not exist among them. It was there, of course, as it had been all along. I had not seen it before, however, even though I had been happily finding and counting colonies by watching for their tents! I did not see it because I had been caught in the snare that lies in every research path: inability to get outside one's previous conceptual framework. Because every entomologist *knew* that tent caterpillars occupied box-like or pyramidal tents, I had paid no attention to tent shapes in my earlier surveys. Consequently, I saw them properly only after I had a strong incentive to look.

This second break-through of the investigation was a happy accident, therefore, and not the product of deliberate planning that

the first had been. If it had not occurred, however, not much else would have happened during that first season of study, and I would have begun the next with a serious handicap. Consequently, I have emphasized it and the preceding mistake. In fact, this whole sequence of events is a good example of the greatest difficulty that confronts us whenever we engage in frontier research. At the border of the unknown, one *must* consciously strive to escape from the mesh of former frames of reference, and to remain outside the generally accepted range of opinion concerning one's problem, for a very good reason: the problem is rarely what accepted opinion says it is! But the difficulty is that one tries so hard to keep one's thinking free on larger issues that one overlooks the danger of continuing to think about apparently smaller issues in terms of older concepts. This lapse is always dangerous, and sometimes disastrous, because there is *no* small issue at a frontier. And how can one *observe* what does not yet exist as a conceptual possibility (Hanson 1958)?

A new survey soon showed that club-shaped tents predominated in areas that were unoccupied by the expanding population before 1956. In fact, if the new infestations of 1956 were sufficiently far from previous infestations, only club-shaped tents occurred. On the other hand, a larger proportion of pyramidal tents occurred wherever the population had been in residence for several generations. In such areas, some trees contained only pyramidal tents, although there were always some club-shaped tents in any locality.

This information led directly to a testable hypothesis concerning the fate of any local population after its first introduction into an area. It seemed reasonable to suppose that active adults would, in general, produce active colonies, whereas less active adults would produce colonies that were decreasingly active, down to a level where some would be very sluggish. Also, it was already known that these various types of adults differed in their ability to fly. Further observation of their movements made it clear that only the most active could fly far enough to enter remote, previously uninfested areas. Therefore, in a new, remote locality, only active colonies should be produced by these first invaders.

Provided that survival within these colonies was adequate, however, adults that displayed different amounts of activity would be produced from them (since even active colonies contain some inactive or sluggish individuals). Of these, only the active adults would be able to fly away before they oviposited; the less active would have to oviposit closer to their birthplace. The next generation in that locality, therefore, should contain some colonies less active than any of the parent generation. And in subsequent generations, an increasing proportion of sluggish colonies should appear in the locality if emigration of active adults exceeded their immigration. This is what the local differences observed in 1956 suggested, and it remained to be seen what actually happened after 1956.

As working hypotheses go, this first model turned out quite well; i.e., its major statements could not be disproved. Certain aspects of the general population trend and of the local environment

affected the situation in any locality. But within these limitations, only minor amendments to the hypothesis were required. When newly infested areas were sufficiently remote, the first generation in fact consisted entirely of active colonies. In contrast, new infestations established closer to older ones contained some less active colonies in the places nearest the older foci -- a fact, incidentally, that helped to establish maximal flight distances for less active females. In the next generation in an isolated area, however, some sluggish colonies appeared, and their proportion rose during subsequent years until the population included many colonies too sluggish to survive. Similar changes, though further advanced, could be recognized in older in- festations. The end result was always the same: a sudden reduction in numbers, because most of the colonies had died.

In that last paragraph I hurried through the findings of several years, after using considerably more space to outline the sequence of events that led up to them. But this is as it should be, if I am to fulfil the intention outlined in my introductory remarks. All the foregoing results have been published, along with many others I have not mentioned here (Wellington 1957, 1960; 1964, 1965). But until now, I have not described how I reached them. And it is reasonably correct to say of this, as of all scientific work, that most of the original thinking had been done by the time the first experi- ments were completed. After 1956, the speculation and reasoning that had led to the first tentative proposals were buried by the pedestrian process of testing them.

Finally, I should point out something not emphasized earlier, though it is implicit in much of the foregoing description. Although this was, and is, a field study of a population, the laboratory has had a strong influence on its inception, direction, and findings. My original dissatisfaction with population theory and practice stemmed partly from the fact that laboratory studies of insect behavior made me sceptical of some of the ideas and conclusions of population ecologists. Many of the clues on how to approach the problem I wanted to investigate came from laboratory observations, as did the evidence for the initial differences. Similarly, the different tent-shapes were detected only by studying colonies with controlled compositions; a method that is still more common in laboratory studies than it is in the field.

And this brings me to the point I wish to make. I believe that laboratory studies by themselves often degenerate into the pursuit of trivia. But I also, believe that field studies that lack the benefit of the special discipline that comes from laboratory training and planning are unlikely to advance much beyond the speculations with which they begin. In other words, the theory and practice of population ecology should not be exempt from the general rule that hypotheses are better disciplined by experiment than by faith and reason (Chitty 1957). Consequently, when we cannot combine labor- atory and field studies during population research, we should at least take the discipline of the laboratory with us when we go to the field.

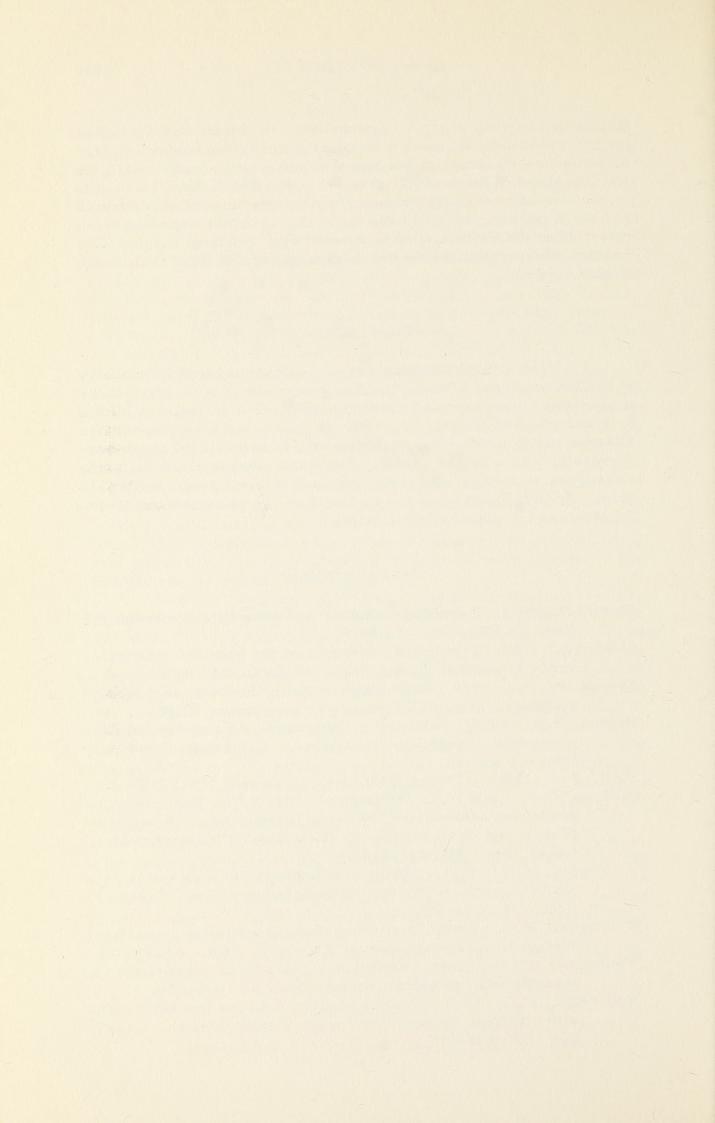A balanced program of laboratory and field investigations in

fact has some very practical attractions. In the studies described here, I was able to do much more during the 1956 season (a matter of some two months) by keeping the laboratory stocks and tests slightly ahead of the equivalent stages in the field. Thus I was able to make any number of mistakes during the first round of experiments and observations, and still have time to correct them by using fresh material as the field population entered each required stage. This enabled me to exploit the two break-throughs of that first season with minimal delay.

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