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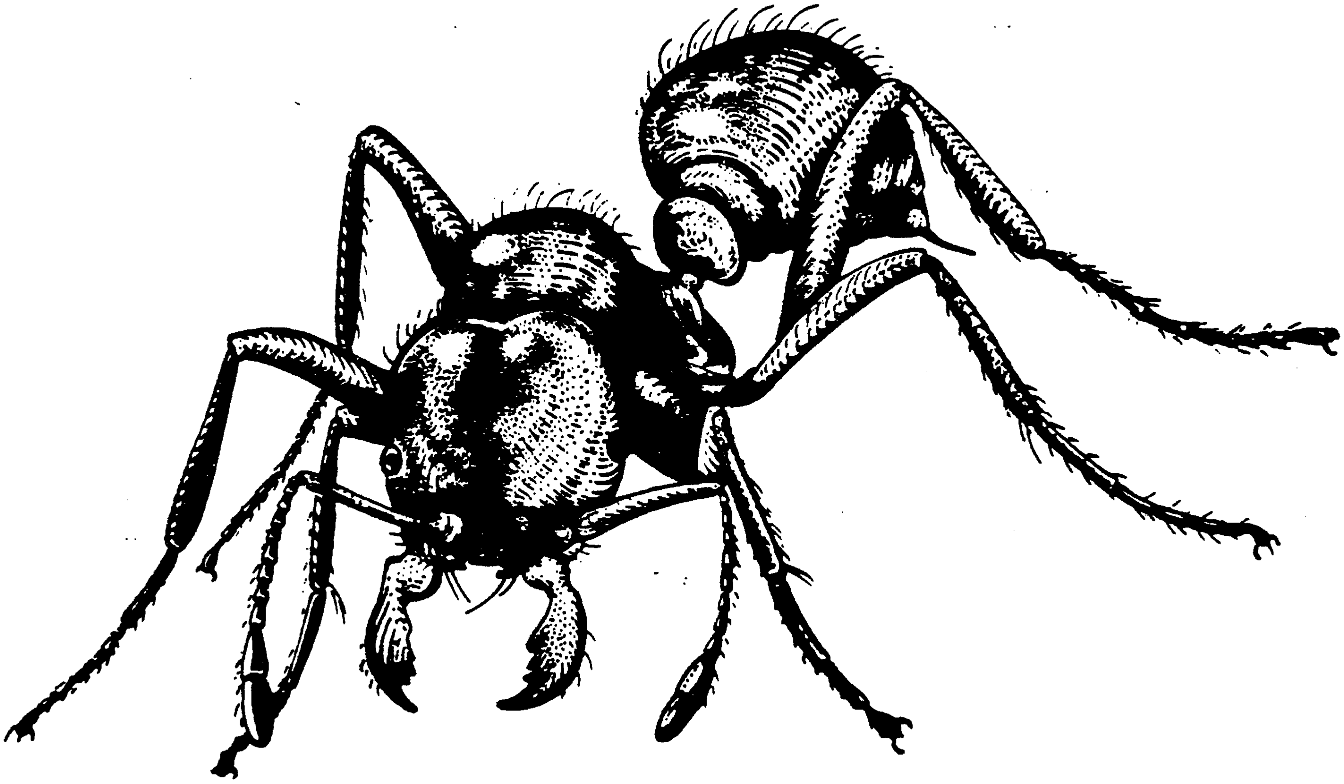

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PANEL II

THE THEORY OF POPULATION DYNAMICS

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INTRODUCTION

When studying a group of insects, we are often overly impressed by their presence and number. When numbers are high, economic entomologists usually locate the point of highest density and count the individuals. From this estimate, the "outbreak" is characterized and control recommendations are presented, with the underlying belief that if sprays are applied at points of highest density, we will get the most kill for control cost and therefore the most benefit. The complex interactions of a pest population with its biotic and abiotic environments renders these assumptions and approaches to a useless leftover from the chlorinated hydrocarbon era. The lack of understanding about the interaction of individuals within a population leads to many, often counter-intuitive, outcomes. For example, every individual will die from natural causes without human-imposed controls. Thus, killing a pest with a pesticide usually brings about damage control through population reduction, but not population control. This fact appears trivial, but perhaps is the most significant point in population dynamics.

THE THEORY OF POPULATION DYNAMICS

When considering the applied and theoretical aspects of insect populations, the organizational levels where interactions occur should be considered. Basically there are four levels of generalized pest insect groupings: subindividual, individual, population, and community. Difficulty raises when observations are made at one level and the implications are projected to a different level. The key to understanding most "single-organism" populations is the population; therefore, individuals must be counted. This simplistic idea becomes a complex issue with social insects or what might be considered as "multi-organism" populations.

For the purpose of this report, we can define "population dynamics" as a discipline that studies the factors producing change in the number and quality of individuals. The term "population" as it relates to insects is ill-defined and takes on meaning only from the context in which it is used. As such, one ecological definition might be: a population is a group of individuals sharing a common gene pool. Unfortunately, the operational definition is usually: a population is a group of individuals occupying an area defined by our concern for considering it as a population.

Thus, a crop pest becomes defined as a population with little concern for its linkage with other individuals outside the crop. This operational differential may be a philosophical side effect of using pesticides. Pesticides applied to the crop kill a large number of insects present or soon to arrive. Defining the population as individuals living or dead in the crop results in high kill statistics. If 1% of a population resides in a crop and 99% are killed, it is not very impressive to state that slightly less than 1% of the population was destroyed.

In a community, groups of individuals live together in some sort of natural order. The temporal and spatial aspects of a community do not need to coincide with a specific population. Communities are complex biological, social, and ecological webs. Managing such structures could be the most important, and largely untapped, non-chemical control method for any species. Thus, community structural modification research should be a high priority.

Adding the word dynamics to population implies a change over time. To understand this, it is essential to realize that a population is distributed over time and space. The spatial distribution is normally used during pest surveys, with results expressed as pests per sample, pests per field, etc. The temporal aspects such as age structure and population maturity and distribution, are seldom addressed even though they are equally important. Both spatial and temporal aspects of a population interact in a way that appears to be opposite or in conflict with simple intuition.

For example, Figure 1 is a typical problem associated with sampling insect numbers to compare spatial differences. The population remains relatively constant until March, when it reproduces rapidly until May. Natural mortality causes a decline until November. Sampling this population would result in densities varying from 10 to 60 on this theoretical curve. The significant parameter represented by this graph is not the six-fold difference in density, but the generation index of I equal to one where I = (density March 1, year 1) ÷ (density March 1, year 2) = 1. This population has not changed, but its calculation required both time and spatial components to be accounted for. Population diagrams invoke the analysis of number over both time and space. In essence, timing of such measurements is critical to getting a true picture of the insect's population. As simple as this idea is, however, it is rarely practiced.

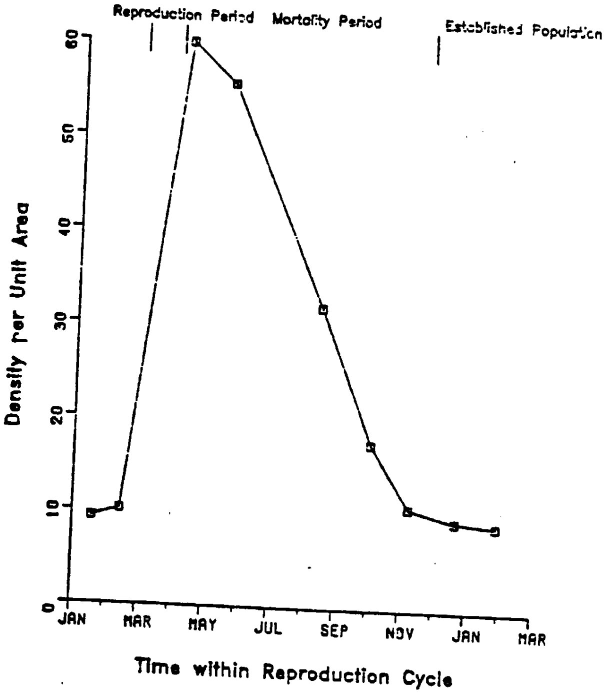

Figure 1. Example of an insect population density through time.

Most historic literature in animal ecology has analyzed factors that limit or control population numbers, and the relative importance of abiotic and biotic components of the habitat have been argued. Only recently have individual populations and community structure been linked in highly interdependent models representing natural systems. Linkage between abiotic factors and the biotic components of the ecosystem can be direct and indirect, with or without time delays. Since these linkages and interrelationships are often complex, a sound theoretical framework is helpful for interpreting the effects that management practices may have on population performance and community structure.

DIFFERENCES IN PESTS

In American agriculture there appears to be four classifications of "emergency pest problem," each requiring a different pest management response:

1. Exotic pests: These are newly-introduced pests whose populations rapidly expand to high numbers before slowly adapting to the new environment. Insects in this category are cereal leaf beetle, gypsy moth, imported fire ant (IFA), Japanese beetle, winter moth, European pine sawfly, Essex skipper, European skipper (McNeil 1975), and alfalfa weevil.

2. Native pests with cyclic outbreaks: Because they are so closely tied with the environment, these pests go through periodic outbreaks. Pests in this category would include spruce budworm, grasshopper, range caterpillar, hemlock looper, bark beetle, etc.

3. Native species with expanded range: This pest species exists in limited geographic areas or environmental habits and adapts to new hosts or climate conditions. Insects such as the Colorado potato beetle, bean leaf beetle (Dietz et al. 1976), apple maggot, boll weevil, and corn rootworm belong in this category. Included could be pests developing additional generations in response to agricultural production practices, or the release of resistant varieties (e.g., Hessian fly). Pests developing resistance to chemicals also could fall with this category.

4. Induced outbreak: This category includes most secondary pest insects that build up in pesticide-impacted environments when the pesticide is not directly applied for their control. The category would include such pest species as spider mites, aphids, and numerous lepidopteran pests.

The response by governments and similar institutions to pest outbreaks needs to carefully consider the unique population characteristics associated with each category. An effective management response may be very different for each situation, and a single control option may have very different outcomes in different classifications.

ECOLOGICAL PHASES OF INTRODUCED PESTS

In this section, we will track the ecological progression of an introduced (exotic) pest as it adapts to its new environment.

During a new introduction phase, the insect rarely is adapted to or closely coupled with the ecosystem. At this time, the abiotic environment exerts several pressures on the insect population. It determines the physiological limits for colonization and whether the insect will survive. Understanding the physiological limits will help determine how successfully the species will colonize. Knowing how climate affects survival and movement will help determine how effective a pest the insect might become. Also, understanding the abiotic effects on the population will aid in predicting whether the new introduction or indigenous species, occupying the same niche, will be favored in a competitive interaction. These predictions will be useful when evaluating management tactics. For example, a broad spectrum biocide that disrupts existing communities could lead to a more successful establishment of an introduced species.

After the new introduction phase, insects go through a physiological adaptation stage. Life table analysis of this phase could indicate windows of vulnerability in the pest's life system, such as periods of stress. Exploiting these vulnerable times could result in successful management strategies (i.e. disrupting overwintering sites). Included in this phase is genetic adaptation. During colonization, insect pests are subjected to new selective pressures as a consequence of changes in the abiotic and biotic components of the environment. Populations that succeed in surviving the genetic selection may have acquired a radically altered, balanced, genetic system. Such genetic evolution is observable in terms of morphology, physiology, behavior, and life history traits. The alterations can be so drastic that the introduced population can be considered to be a new race or even a new species, complete with pre- and post-mating isolating mechanisms. In terms of pest control, this means that an introduced species has, in its new environment, the potential to evolve in an unforeseen manner (Templeton 1979).

The final phase of colonization is the successful physiological adaptation of the insect. At this time both competitive and predator/parasite relationships are important, which typically results in the pest status of the introduction being less than the previous stage. Again, abiotic factors may alter competitive relationships between the pest and its natural enemies.

By knowing the effects that weather, community structures, and their interactions have on pest populations, it is possible to predict when and where pest populations will occur. This information also can be used to avoid control tactics that adversely disrupt the system. Humans can greatly impact the natural evolution and adaptation of exotic species to its new environment by stopping and, in some cases, reversing this natural progression.

THE WORLD: A BUG'S POINT OF VIEW

Elephants and hippos do not get caught in water surface tension. Insects do. Understanding the needs and dynamics of a population requires that we imagine things in the way that a species must see them. The microclimate experienced by a particular species is not necessarily that reported by the U.S. Weather Service or measured in a weather shelter. Often that species has evolved over millions of years to become adapted to a particular environmental niche. The fact that is becomes a pest may simply be a consequence of our inadvertently expanding its niche space a million-fold or so with bulldozers and tractors or accidental movement. When this happens, we might consider possible ways to shrink the microclimate niche space. If this can be done while still achieving system goals, then the pest may be reduced to non-pest levels. Understanding the microclimate of the pest could lead to the development of interesting management options. The literature is replete with such examples.

OPPORTUNITY IN A CRISIS

A unique opportunity exists in social insects to research the effects of individual quality on population dynamics. By defining a colony of social insects as an "individual," the individual quality and its effects on the population of such individuals becomes easier to research and model. Model resolution increases. In fact, for a community of ant species, many levels can be identified and measured fairly easily. Levels start with a species; within a species there is an age of nest; within that level there is a distribution of ant types; and within that level there is an age distribution. This complexity is measurable for most insect populations only with enormous resources. For ants, however, the within-nest dynamics can be measured and studied fairly easily; the direct effects of changes of within-nest distributions (age and type) can also be modeled. Such models will help integrate a research program much more than is usually possible. With increasing complexity models become more realistic, which increases the level of understanding of the population and its interactions. This is particularly true when measuring abiotic stress on within-nest dynamics. Models that effectively incorporate abiotic stress are difficult to develop for non-social pest populations.

POPULATION ANALYSIS

Measuring an Abstraction—Determine Sampling Attributes

All populations share certain life processes. For example, the development rate of all insects is temperature-dependent. Thus, both physiological and chronological time scales should be used when measuring life processes. Many processes that occur (e.g., reproduction, mortality, movement) are related to the density of the target species and/or other species.

An important concern in dealing with social insects is that different processes affect the individual and the colony differently. Understanding the individuals' dynamics does not necessarily imply a knowledge of colony dynamics and vice versa. Because of this hierarchy, it is imperative that processes be examined at the appropriate level. Thus, if one is concerned with managing a social pest and the target is the colony, colony dynamics should be most closely examined. Given this background, the major sampling considerations are:

(a) selecting the sampling entity (individual, cluster, colony),
(b) selecting the sample unit (square meter, soil type, habitat, etc.),
(c) selecting the spatial and temporal sampling intervals,
(d) determining the type of distribution(s) observed and any changes associated with other population and habitat characters, and
(e) calculating the sampling schemes for various specific objectives.

All sampling plans must provide error estimates and make variance partitioning possible. The necessary data to establish these sampling attributes can come from early phases of concurrent research that includes changes in (1) the pest: numbers of individuals and individual attributes, and (2) the environment: physical and other organisms (plants, competitors, enemies, and commensals). In social insects, where the unit of study may not be the individual, nest or colony characters have to be measured to give the colony some specifically identifiable states (i.e., all colonies are not equal). These studies should be conducted extensively (coarser sampling over wide areas) and intensively (including the extreme situations).

Population behavior of new invaders, such as the IFA, may change dramatically through time. Inferences drawn from the study of invading populations along the advancing front of an infestation must be interpreted cautiously. For example, populations of the sea lamprey virtually exploded when the species reached the Great Lakes. Despite aggressive control efforts, predation on lake trout devastated that fishery. Now, however, lamprey predation is scarcely a factor in the booming sport fishery for the several salmonid species introduced from the Pacific. For this reason, it is particularly important to encourage studies explicitly designed to detect and interpret long-term changes in population behavior. Specifically, some areas should be reserved for long-range (perhaps 20 to 30 year) studies on the population dynamics of the IFA.

From this work, correlations can be found between the pest and its environment. Typically, these become the basis for generating hypotheses about cause and effect relationships. These hypotheses need testing. As correlations are developed, emphasis should shift toward experimental studies designed to test these hypotheses, rather than to assume their validity. Initial research should concern hypotheses that appear most crucial to conceptualizing the pest system. Since more than two alternate hypotheses may explain any single correlation, the researcher should consider all hypotheses and design research to differentiate among them. Once a given hypothesis is confirmed, the general conceptualization should be updated.

At any time, both the scientist and the granting and/or regulatory agency can use this construction when making judgments on current research or management requests. However, both the researcher and involved agencies should avoid (1) studying only those aspects that have immediate management applications, or (2) continuing, ad infinitum, studies of relationships having no known potential for management.

ANTS AND WHAT TO LOOK FOR— A PARTIAL LIST

As in all other cases, the attributes of a system are determined by the questions and hypotheses guiding the study. The following example concerns the community dynamics of ants. Since the level of study has been defined at the community level, measurements are restricted to processes that feed into determining community dynamics. Thus, many features may be excluded entirely and treated as a "black box." For example, for some purposes, the mechanisms of pheromone production and distribution within a nest may be ignored; integration of nest activities becomes a product of a "black box" hormonal system. However, the decision to exclude the mechanics of a process has to be chosen carefully. For example, ignorance concerning the functional details of mammalian hormones may be acceptable when studying the interactions of ungulates, but it would be essential to rodent interactions where adrenal gland weight and activity relates to behavioral dominance. The point is to be cognizant of the role of hormones/pheromones in ant community dynamics and to carefully choose the level of measurement that meets the requirements of the guiding hypotheses and questions.

Some examples and rationales for selecting sampling attributes of community dynamics of ants include the following, very incomplete, variables.

1. Species-specific foraging behavior: Shifts in the time or location of foraging in the presence or absence of other species (e.g., McNeil et al. 1978) may indicate important competitive interactions and could, under some circumstances, feed into the community structure.

2. Spatial distribution of nests: For this study, movement of workers of the same species from nest to nest validates the use of the nest as the sampling attribute. The distribution of nests of each species and their abundance through space and time is the appropriate sampling unit to measure the outcome of community interactions. The distribution of foraging workers around each nest may be the more appropriate sampling unit for measuring the interactive mechanisms of community change.

3. The dynamics of the community: Change, resistance to change, and rates of return to the original community composition are the focus. Therefore, experimentally, nest distribution is appropriate. For meaningful results, conditions must be specified (e.g., which environment, over what time course, the initial set of populations, etc.).

SOCIAL INSECTS:
PROBLEM OF DEFINITION AND BIOLOGY

Relative Time as a Problem and Opportunity

For most pests in annual cropping systems, the periodicity of the habitat is long relative to the generation time of the pest. With many species, the reverse is true. The lifespan of a particular crop is generally shorter than the generation time of the resident social insect colony. Short-generation pests that spend much or all of their lives in a single environmental patch should follow the environment closely (i.e., become specialized for particular field types). Long-generation pests and pests with low dispersal thresholds should be relative field generalists. Thus, habitat manipulation as a control procedure for long-generation pests may have limited success unless the alternating habitats (in time and space) are chosen on the basis of knowledge concerning environmental determinants of population dynamics.

Population Processes

Birth-death processes in social insects are similar to other organisms, but some important differences exist. Obviously, the addition of sterile workers is simply individual growth of the colony; the colony is the organism from the perspective of population dynamics. As the colony adds or subtracts workers and adjusts the caste composition, the colony changes its ability to meet the various life contingencies of reproduction (new sexuals leaving the colony), competition, nest repair, etc. That is, the colony has various age or stage-specific parameters. In cases where queen substitution occurs, the colony is, in principle, immortal. Concepts, such as reproductive value, become stage-specific properties, and "life" expectancies become the set of transitional probabilities of death associated with each stage. The possibility of polygyny (multiple queens) occurring in social species means that fecundity will be highly variable within a species; it then becomes necessary to treat variance as a parameter in a life system model. Death of queens in polygynous colonies is treated as an effect on reproductive value. This explanation of birth-death processes illustrates the equivalent processes in social and solitary species. These processes, however, may be difficult to measure.

The colony is a responsive homeostatic system with many paths for feedback loops and mechanisms for controlling flow rates along the loops. For example, a colony has four levels of buffering against the morbidity effects of a variable food supply.

1. The colony can store food in the nest; therefore, foraging and harvesting rates are not limited by the immediate metabolic needs of the colony. Furthermore, saturation curves for foraging behavior may not be closely correlated to colony biomass but may be limited by environmental, temporal, and spatial patterns of food availability.

2. The ability to change foraging behavior relates to the abundance and distribution of food outside the nest. For example, an ant colony may forage by using a few well-defined trails when food is predictable and clumped. When food is unpredictable and dispersed, the colony may switch to diffused foraging behavior without defined trails.

3. Larval secretions may be used to feed other larvae and workers, which distributes the food within the colony to prevent local shortages among some larvae.

4. Larvae may be cannibalized (actually a form of colony catabolism) as food for other larvae. There is considerable fine tuning in this behavior. For example, since eggs have received little colony investment, they are the first stages to be used as food. Sexual larvae are fed preferentially, thus maintaining reproductive success.

Relatively little seems to be known about the population dynamics of social insects. Even age at death, a straightforward attribute of individual insects, may be difficult to define for a colony or nest. While the members of this panel had relatively little experience dealing analytically with such unique attributes, they judged that current analytical methods can easily be modified to incorporate these unique features.

GENETIC CONCERNS: A CASE OF NEGLECT

Problem or Opportunity

Genetic systems of social and non-social insects are similar in some respects, but different in others. In non-social insects, bisexual reproduction of diploids maximizes genetic exchange and thus maintains a high level of genetic heterogeneity in the species. In social Hymenoptera, males develop from fertilized eggs and are haploid; the females, from fertilized eggs, are diploid. This genetic system is known as haplodiploidy (Wilson 1971, Crozier 1977). A connection between haplodiploidy and the frequent occurrence of sociality in insects has been suggested by several researchers. This system allows considerable inbreeding and thus maintains a high degree of homogeneity among social insects. Recent biochemical evidence from gel electrophoresis of isozymes reveals that the average heterozygosity of social insects is considerably lower than that of non-social insects (Crozier 1977, Ayala 1982). Such low genetic variability in social insects confirms that there are specific differences between the genetic systems of social and non-social insects.

The development of social systems involves many changes in the characteristics of social species that are not found in non-social insects. Many behavioral and ecological interactions that are integral parts of a social system have no parallel in non-social insects. Regarding the reproductive potential, social insects are often thought of as having unusually high fecundity. The task of reproduction in social insects, however, is carried out by one or a few reproductives; in non-social insects, all females contribute to the reproductive task. When comparing populations, the reproductive potential of the two insect systems is probably similar. A special feature of social insects is that the reproductives are protected in the nest and are seldom subjected to adverse environmental conditions. Since most of these species have a long generation time, they are less affected by natural selection pressures. This may be one of the reasons why social insects appear to develop resistance to insecticides at a much slower rate than non-social insects.

Community Analysis

Performance of a population depends on the combined effect of the individual attributes of the population plus the total interactions of other populations occupying the same geographic region. Analysis of the nature of the interactions between populations, and the results of these interactions in terms of stability, persistence, and dominance, is the topic of community ecology. Community ecology, therefore, can be used in understanding the effects of complex interactions (i.e., competition and predation) on the abundance of particular pest populations.

For an introduced pest, which progressively becomes more adapted to new ecological associations, particular community-level associations may be more important during certain phases of adaptation than at other times. For example, during the early stages of colonization, competition with native species occupying a similar niche would be the most important community-level association. In later phases of adaptation, relationships with natural enemies would become important.

A CASE FOR MODELING

Our understanding of the actual population dynamics of organisms can be greatly enhanced by considering the diversity of behavior of population models. Even very simple models of a single species can exhibit a vast array of possible behaviors. This type of complexity can usually be obtained by varying the "constants" in the model, which is analogous to making them functions of time or space in a very general sense (to what actually happens in the real, "non-constant" world). That very simple models of one or two species exhibit complex behavior when subjected to this type of analysis is encouraging to the population biologist. It implies two things: (1) predicting complex behavior of the real world is within the scope of relatively simple models, and (2) real world complexity can be reduced to simple components.

Simplistic population models showing that a wide array of behavior is possible also says something to humans about population management—ecological communities will not have simple responses to simple inputs. Surprises will be the order of the day. There are no simple rules—just exceptions. Good management is possible, but it must be long-range and founded on knowledge. Given the complexity of the simplest ecological community, ill-considered, forceful, management attempts will simply produce large perturbations with uncertain consequences. The worst enemy is ourselves—our haste for a quick, simple solution, rather than a desire to understand the problem (Stinner 1982).

HIGHER ORDERS OF INTERACTION

The environment largely determines how a community will move through time and space. By varying the "constants" in simple models, very complex behavior can be obtained. Therefore, when these "constants" in a community are actually environmental functions, the environment drives the community dynamics. Even the most gross level of dynamics (e.g., establishment of a new species) is obviously a function of temperature, rainfall patterns, etc. Therefore, it should not be surprising that even simple species interaction models display remarkably different behaviors in response to only one variable, like temperature. As temperature changes, a pest and its natural enemy may change in their interaction from damped cycles to constant cycles to increasing cycles to chaotic behavior. This change in behavior could occur over the course of an annual cycle or over the species' geographic range in response to temperature. We must understand that simplistic thinking about biological responses to environmental influences is not likely to be correct. The rich diversity of possibilities will not be predictable.

In agricultural systems, perhaps excluding tree crops and permanent pastures, communities of pests are unlikely to be at near-equilibrium conditions. Under these conditions, much community ecology theory is inapplicable. The appropriate development of a theoretical basis for an agricultural community ecology should consider the following:

1. Perturbation analysis with an emphasis on resistance and resilience.
2. Methods of analysis, e.g., loop analysis as developed by R. Levins, appropriate to complex systems where many interactions can be expressed only in qualitative form.
3. The relationship between changes in the connections between species and what happens to the form of stability. This requires an analysis of the hierarchical pattern of species links within the community. It is important to identify subsets that are connected to the rest of the community by single links.
4. The relationship of resource utilization curves as a function of community composition and local habitat. In other words, in which habitat and for which permutation of species mixtures do we find minimum and maximum overlaps in species resource utilization curves.

The goal is to develop procedures and generalizations such that community level management can systematically and predictably determine the probability of invasion by a new species. With regard to the IFA, it is frequently asserted that no natural enemies or important competitors exist. Since the IFA is abundant and expanding its range, the IFA seems to be independent of competition and predation from other species. However, this assumption ignores the reality of considerable local variation in nest density and colony abundance. When the IFA is abundant it is said to lack competitors and predators, but when it is scarce, the IFA is said to be in a "poor habitat." Thus, the possibility of biotic controls on IFA population dynamics is semantically excluded. Clearly, the proper natural laboratory for the study of the population dynamics and community ecology of a pest is across an array of habitats where the proportional representation of the pest in the community ranges from "frequently absent" to "usually abundant."

CONCLUSIONS

Research and Resources

As applied biologists, we often have heard: "The problem is here now! We must do something! We cannot wait for research." If this policy of ignorance were only words and not subsequent budget adjustment, there would be more hope. There are at least two ways to manage crisis: one is to prepare a program of action in ignorance, and the other is to prepare a program where at least one outcome is a significant increase in our understanding of the problem. Research does not have to be considered as a noble human endeavor conducted outside of immediate need or, conversely, conducted solely for the purpose of immediate application. Both approaches perpetuate our initial ignorance for future consideration. Neither has a high probability of success. Our lack of basic understanding of IFA population dynamics after more than two decades of government response is a specific case in point. The policy, "the only good insect is a dead insect," has not worked and cannot be expected to work. *It should be a given policy that, in any control response (eradication, containment, management), failure is possible.* Thus, modest funds should be provided for long-term study of the population dynamics of the species at the onset (or certainly within six months) of eradication attempts.

Historically, there has been a strong reluctance to provide these funds since it admits potential failure of the present program. If it was a general policy to provide research funds, then the political problems associated with an admission of potential failure are avoided. All efforts at challenging a newly invading species should include an initial conceptualization of the population dynamics of the species. This construct must be flexible and should be updated as new information is obtained.

To blame institutional response totally for perpetuating biological ignorance of invading pests would be a gross oversimplification of the problem. Clearly institutional inertia and political expediency are dominant factors in resource allocations for program development. However, the lack of resources for basic population research cannot be strongly implicated in closing minds or the inability to conceptually interpret existing information and theory related to other animal populations.

Economic entomologists and pest control specialists in particular dwell on the uniqueness of each pest subdivided into each crop. If, on the other hand, biologists were looking for theoretical bases for examining apparently dissimilar events, a great deal of information could be brought to bear on particular problems. The case in point is that IFA research should look for population principles in other pest species instead of treating IFA characteristics as if they were unique.

Single Factor Control

In given pest situations we tend to attack the pest directly with mortality agents whose action is often non-specific. Natural enemies, competitors, and disease agents may be exerting a very high, and continuing, mortality on the pest despite its pest status. If this complex is disrupted, the pest, usually having a high reproductive potential, is released from much of its mortality pressure. The result is the often observed pest resurgence phenomenon; in addition, new pests can be created by indiscriminately removing their mortality agents. Thus, knocking out a section of a community without being sure of what will happen can produce undesirable surprises.

Community Structure

We must understand and manage at the community level. We are part of the community that we seek to manage, and we cannot escape its feedback if we completely ignore its structure and proceed in heavy-handed ignorance. The scientist needs time and support to obtain the basic knowledge necessary for any intelligent management program. Large-scale programs covering millions of acres should never be undertaken until a high level of understanding of the system has been obtained. In fact, in many situations, once that level of understanding is obtained, we will probably have resolved the system into several sub-systems each requiring a somewhat different program of management. There are few simple solutions to managing community ecosystems. If we apply the intelligence we have to the management of ecosystems, we probably can be successful in many cases. If we do not apply that intelligence, it is most likely that the ecosystems we seek to manage will control us.

Genetic Analysis

Genetic analysis of insect populations, especially pest species, has been a neglected field of research. Extensive research data will be needed before any generalization can be made about the genetic systems of pest species. Since population is the basic unit of ecology and evolution, the study of genetic variation should be focused at the population level to determine the genetic components that influence population processes. Many fruitful approaches are available for genetic analysis of social and non-social insects. Techniques such as chromosomal karyotype analysis, gel electrophoresis of isozymes, and DNA sequence should be routinely used for genetic studies. In addition, various ecological, physiological, and behavioral traits of pest species should be monitored to determine population variations. Traditional crossbreeding experiments will also be needed to define genetic mechanisms of inheritance. Since most of these studies require a long time, adequate duration of time and financial support must be available for such research programs.

Evidence of high genetic variability in insects reflects the tremendous evolutionary potential of pest species; control programs should be designed with this in mind. Probably no single perfect control method exists against an insect pest since the insect is likely to evolve resistance. However, evolutionary theory predicts that an insect pest is far less likely to evolve resistance to a control program where many strategies are used. In general, therefore, a control program that incorporates multiple approaches is the best type of program. In order to employ multiple-approach control strategy, basic knowledge of the ecology and genetics of pests and related species must be available, and only through application of such knowledge can the control options that exist and their respective risks be dealt with. Therefore, for the development of a long-term control program, there is an immediate and critical need to increase basic research on the ecology and genetics of pests and related species.

RECOMMENDATIONS

1. Funds should be provided for long-term study of the population dynamics of the pest species at the onset of any eradication trials for any pest.
2. Research on the IFA should examine the population dynamics of other pest species and compare them to the IFA.
3. Single-factor control should not be a priority in control strategies, rather emphasis should be placed on multi-factor management strategies.
4. A conceptual framework for dealing with the population dynamics of the IFA needs to be developed.
5. Modern experimental design, analytic, and measurement tools should be used to study the population dynamics of the IFA.
6. A workshop of researchers studying population dynamics of the IFA and of other species should be held to pool knowledge and develop a sound system for studying

the population dynamics of the IFA.

REFERENCES CITED

Ayala, F. J. 1982. The genetic structure of species. pp. 60-82 in Milkman, R. (ed.), Perspectives on Evolution. Sinauer Associates, Inc., Publ. Sunderland, MA.

Crozier, R. H. 1977. Evolutionary genetics of the Hymenoptera. Ann. Rev. Entomol. 22:263-288.

Dietz, L. L., J. W. Van Duyn, J. R. Bradley, Jr., R. L. Rabb, W. M. Brooks, and R. E. Stinner. 1976. A guide to the identification and biology of soybean arthropods in North Carolina. N.C. Agr. Exp. Stn. Tech. Bull. 238. 264 pp.

McNeil, J. N., J. Delisle, and R. J. Finnegan. 1978. Seasonal predatory activity of the introduced redwood ant, *Formica lugubris* (Hymenoptera: Formicidae) at Valcartier, Quebec, in 1976. Can. Entomol. 110:85-90.

McNeil, J. N., R. M. Duchesne, and A. Comeau. 1975. Known distribution of the European skipper, *Thymelicus imeola* (Lepidoptera: Hesperiidae), in Quebec. Can. Entomol. 107:1221-1225.

Stinner, R. E. 1982. La lutte integree—une perspective. Phytoprotection (in press).

Templeton, A. R. 1979. Genetics of colonization and establishment of exotic species. pp. 41-49 in Hoy, M. A., and McKelvey, J. J. (eds.), Genetics in Relation to Insect Management. Rockefeller Foundation.

Wilson, E. O. 1971. The Insect Societies. Belknap Press of Harvard Univ. Press, Cambridge, MA. 548 pp.