Chapter 3

Discussion:
From Individuals to Populations

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Processes operating at the level of individual organisms can determine the properties of populations, communities, and ecosystems. Theoretical studies can play an important role in advancing our understanding of the connection between organismal-level performance and patterns at the ecological level. In this paper I will first report our discussion of approaches to the area, including the roles of mechanistic versus phenomenological models, the interplay of theory and empiricism, and the usefulness of simple models and microcosm studies in understanding a complex world. I will then present a brief summary of examples of organismal-level analyses that have contributed to our understanding of ecological phenomena, and will conclude with a report of our discussion of directions for future research. This paper does not represent my personal view of this field, but rather attempts to report the range of opinions expressed during our meeting.

APPROACHES

Mechanistic versus Phenomenological Models: Why Should We Worry about an Individual When We Are Describing a Population?

Some models are phenemonological descriptions of a system, whereas other models seek to understand the essential processes governing components of the system and to build up from such a basic understanding of underlying mechanisms to an overall description.

A number of arguments can be made for focusing on phenomenological models (e.g., Rigler 1982). Using phenomenological regression predictions, one has some hope of getting answers in a timely fashion. For example, it is more

reasonable to use such a model of birth and death rates to forecast the human population next year than it is to try to understand all the reasons that people decide to have children or to drive while drunk. Furthermore, often even elaborate mechanistic models do not match the data as well as some very simple phenomenological regression models (e.g., Gross, chapter 1). Why, then, should we worry about individual function or burden ourselves with the more cumbersome mechanistic models?

The limitations of phenomenological models render them inappropriate for certain types of analyses. Whenever we make a prediction using a phenomenological model, we implicitly assume (1) that conditions do not change, and (2) that the phenomena that go into the model adequately sample the causal pattern of interest. Therefore, phenomenological models are best used for making short-term predictions. For example, although it is sensible to use phemomenological descriptions of fertility rates to predict human population growth on the time scale of decades, it is necessary to understand important aspects of the physiology and behavior of individuals (such as how reproductive physiology is affected by factors like intervals of breast-feeding, or the interplay of workload and nutrition) to understand what may have held hunter-gatherer populations in balance for thousands of years. Similarly, regression predictions of the spread of a disease such as AIDS are useful for the next few years, but longer-term predictions should be made based on an understanding of the dynamics of the behaviors of individuals that transmit AIDS (May and Anderson 1987). Furthermore, conditions do not even have to change for phenomenological models to break down if a system is regulated chaotically—a system can be characterized by two regular patterns between which it can suddenly shift. Another major limitation to the use of phenomenological models is that they can be applied only to systems for which data are already available. Today man is contemplating perturbations to unique and irreplaceable ecosystems for which we have no data on which to base phenomenological models; in such cases mechanistic models have to be employed.

Although mechanistic models may not fit the data as well as phenomenological models and may be complicated and slow to provide answers, the development of mechanistic theories can lead to increased understanding of how a system works. A number of examples of how mechanistic models have provided ecological insights are reviewed by Schoener (1986). Note that one important lesson we have learned even from simple linear mechanistic models (such as the physical laws governing the motion of a pendulum) is that something that is rigidly determined can essentially be unpredictable if it is sensitive to initial conditions. Such mechanistic models point out the importance of history and stochastic processes in determining the course of events, even in systems for which we know the rules governing behavior.

A further discussion of the pros and cons of phenomenological versus mecha-

...ric models can be found in Peters (1986) and Lehman (1986). Ideally these ...ferent approaches can reinforce each other. Phenomenology helps organize ...servations so that mechanistic laws can be formulated, and these in turn can ...plain the phenomenological rules. There are important problems that can best ... addressed by one or by the other approach, depending on the particular ...uestion being studied.

What Can Organismal Biologists and Ecologists Do For Each Other?

Many mechanistic ecological models assume that particular processes at the organismal level are important in governing the behavior of a system at a larger level of organization, such as a population or community. Examples of such ecological modeling are discussed by Schoener (1986) in a recent symposium about mechanistic approaches in ecology (Price 1986). One important role of studies at the organismal level is that they can tell ecologists factors that can be ignored versus those that must be included when simplified models are developed. In addition, organismal studies can provide information for ecological theorists about the rates at which various processes occur, revealing those that are nonlinear. One important consequence of learning how mechanisms on the organismal level affect the properties of populations and communities is that such knowledge can provide a link between ecology and evolution. Conversely, we cannot understand the evolution of organismal-level traits (physiological, morphological, behavioral) without understanding the ecological context in which natural selection operates.

Interplay between Theory and Empiricism

The interaction of theory and empiricism should be a leapfrogging activity where theories lead to experiments that point out their limitations or disprove them, thereby stimulating new theories and experiments; our understanding of the way a system works is thus improved step by step. As physicists are well aware, the successful theory is one that leads to an understanding of why it is wrong and what should be done next. Although it should be a constructive activity and cause for celebration when a theory is found to be less than perfect, ecologists tend to denigrate theory when models are found to be flawed. We need to recognize that the successful theories are the ones that are kicked out, thereby leading to interesting experiments and new theories. A recent discussion of the psychological and philosophical aspects of the interplay of theory and empiricism in ecology can be found in Loehle (1987). Improving communication between theoretical and empirical ecologists, who often have quite different training, should lead to more fruitful interactions.

What can theorists do for empiricists? One important role of theory is to simplify complex ecological problems—to take the unmanageable and make it manageable. One of the many examples of such simplification is the concept used in some food-web models of a "trophic species," which may encompass a hundred taxonomic species with similar diets, and hence similar trophic roles in an ecosystem. By thus abstracting the essential elements of what is known about a system, theory can point out where to look for the next problem and can instruct empiricists to focus on research systems that are not overwhelmingly complex. Another way in which quantitative theorists can simplify the work of empiricists is by pointing out which of the myriad of parameters that could be measured are the ones most likely to have large effects on the process being studied. Optimization models can reveal whether the "price" of straying from some optimum behavior or morphology is large or trivial, and hence can alert experimentalists to traits on which to focus their attention. One other important job for theorists is to be very explicit about the whole battery of assumptions on which their models are based. Such clarification enables empiricists to judge whether or not a particular model is appropriate for the system they are investigating and permits them to avoid the trap of simply using the model in vogue at the time of their study.

What can empiricists do for theorists? One role for experimentalists is to point out to theorists the important unsolved empirical problems and the unexplained patterns observed in nature. Another job for empiricists is to use their knowledge of natural history to show theorists what they can and cannot ignore as they try to simplify and abstract a system. It behooves empiricists to demonstrate to theorists the relevance to ecological processes of organismal-level details, such as the relationship of nutritional physiology or thermoregulation to foraging behavior, and hence to community structure. A very important service that empiricists can perform is to test whether models have any relationship to what goes on in nature. One aspect of this empirical work is descriptive: the measurement of parameters to plug into models, and the comparison of predictions of models with observations in nature. We need to remember, however, that agreement of nature with the predictions of a theory does not necessarily mean that the theory is correct (e.g., Dayton 1973). Another aspect of empirical evaluation of theory is experimental research: specific hypotheses are tested by controlled, manipulative experiments conducted either in laboratory microcosms or in the field. If theorists want empiricists to test their models, they should build models with *measurable* parameters and *testable* hypotheses. Empiricists need to let theorists know what is "do-able," and theorists should familiarize themselves with how empirical work is done and with the difficulties of experimental ecology (e.g., Platt 1964; Quinn and Dunham 1983; Hurlbert 1984).

The key to the successful interplay of theory and empiricism is communication. It is encouraging that some ecologists do both theoretical and empirical

research, and that close collaborations have developed between a number of modelers and experimentalists.

Simple Models of a Complex World: Theories and Microcosm Experiments

Rather than become overwhelmed by the bewildering complexity of nature, ecologists can develop simplified theories or conduct experiments in manageable microcosms. The hope is that such simple systems may reveal basic principles valid both for and within more complex systems. Experiments using microcosms offer a number of advantages: they can be designed to reproduce the assumptions of a model being tested, and they can be conducted in replicate with appropriate controls. The small sizes and short generation times of organisms such as insects or bacteria make them appealing subjects for microcosm studies. Furthermore, modern microbiological techniques permit us to know a great deal about the genetic variability between individuals in populations of micro-organisms we can use in our experiments. Nonetheless, we must remember that the kinds of questions that we can ask of such organisms are different from those we must ask of organisms with larger bodies, longer lives, and more flexible behavioral repertoires, such as vertebrates.

Although we certainly should first measure processes in and develop theory for simple systems before moving on to more complicated ones, we must keep a number of questions and precautions in mind. If bottle experiments—for example, of predator-prey relations—are made simple enough to mimic the assumptions of a model they are testing, isn't such laboratory ecology little more than analog computing? Such experiments are certainly useful to test models, but are they so unrealistic that they tell us little about nature? Microcosms are by definition smaller than natural systems; how do we decide what scale (spatial and temporal) is appropriate to test theories about processes occurring in natural systems (see Giesy 1978; Powell, chapter 11, this volume; Steele, chapter 12, this volume)? To what extent can the unpredictability encountered in nature be sensibly replicated in controlled experiments? Good lab work must be based on a sensitive appreciation of natural history; otherwise it is all too easy to miss crucial elements of the real system when we bring it into the lab for study. We must also remember that what is considered "simple" is strongly conditioned by the background and objectives of the scientist. For example, a thermal spring community of twenty-five species that seems appallingly messy to a microbial physiologist can appear delightfully simple to a field ecologist.

It is important that we pursue sensible answers to these questions: there is a very specific and growing demand for understanding what we need to do as pilot studies in microcosms prior to the release of genetically engineered organisms.

WHERE ARE WE NOW?

Information about organismal-level functions (e.g., behavior, physiology, biomechanics) has proved useful in understanding ecological processes, and vice versa. Gross and Pulliam (chapters 1 and 2) review a number of studies that illustrate the fruitful interplay between theory and empiricism at this interface between the organismal and ecological levels of organization. In this report I will briefly mention (with a few leads into the literature) some additional areas of research brought out in our discussions, but not covered in those papers, that exemplify the contributions of theoretical work.

Plant Pysiological and Biophysical Ecology

Gross (chapter 1) reviews the physiological ecology of terrestrial plants, but not aquatic ones. Examples of the usefulness of organismal-level physiological information to the development of community-level models of phytoplankton can be found in Tilman (1982) and Powell and Richerson (1985). Discussions of the importance of the physics of nutrient flux at the surfaces of individual cells to questions about the productivity of lakes and oceans can be found, for example, in Jackson (1980) and Lehman (1984). Empirical and theoretical work on the biophysical ecology of marine macrophytes is reviewed by Koehl (1985).

Behavioral Ecology

Aspects of the interface between animal behavior and ecology not covered by Pulliam (chapter 2) are reviewed in Krebs and Davies (1984) and Rubenstein and Wrangham (1986), and a recent synthesis of optimal foraging models is given in Stephens and Krebs (1987).

Animal Biophysical and Physiological Ecology

Another field rich in examples of the interplay of theory and empiricism is the study of the interface between the physical and physiological performance of animals and their ecological function. Rather than attempt to review this growing field, I will merely mention a few examples here.

Analyses of the biophysics of heat and water regulation reveal when and where particular animals can be active, and hence point out constraints on habitat use, on ecological interactions such as competition and predation (e.g., Porter et al. 1975; Heinrich 1979), and on reproductive strategies (e.g., Kingsolver 1983). Conversely, models that incorporate the ecological roles of animals can provide

insights about organismal-level function. such as which animals should be expected to thermoregulate and which should not (e.g., Huey and Slatkin 1976).

Our understanding of foraging ecology and habitat use by animals has also been expanded considerably by analyses of the metabolic costs of various activities (e.g., Heinrich 1979), and by studies of nutritional physiology and chemical defenses (e.g., Rosenthal and Janzen 1979; Crawley 1983; Hubbel and Howard 1984).

Biomechanics (see, e.g., Wainwright et al. 1976; Vogel 1981; Alexander 1983; Denny 1984) also provides ecologists with information about physical constraints on the ecological performance of organisms. One obvious example of the ecological importance of mechanical processes is the role of physical disturbance in structuring many communities (e.g., Sousa 1984). Examples for rocky shore communities of mechanistic studies of disturbance that involve both theory and empirical work include biomechanical studies at the organismal level (e.g., Koehl 1977; Denny, Daniel, and Koehl 1985), which reveal mechanisms responsible for the differences in susceptibility of various organisms to removal by waves, and studies at the community level, which focus on the ecological consequences of this removal (e.g., Paine and Levin 1981). Biomechanics has also shed light on other ecological questions. For example, flight aerodynamics provide a mechanistic explanation for the patterns of hummingbird foraging in habitats at different altitudes (Feinsinger et al. 1979). Similarly, a mathematical model of the biomechanics of nectar feeding led to predictions of strategies of foraging by hummingbirds and of nectar production by plants (Kingsolver and Daniel 1983). An analysis of the mechanics of silk webs proved necessary to understand habitat use and foraging by spiders in a tropical forest (Craig 1987). Similarly, patterns in habitat use and foraging by fish of different body forms can be related to the biomechanics of swimming (e.g., Webb 1984). Conversely, ecological analyses can make sense of otherwise puzzling biomechanical features. For example, the abundance on wave-swept reef crests of a species of coral with a "bad" (e.g., breakage-enhancing) mechanical design was explained by an ecological study that showed breakage to be an important mode of asexual reproduction and dispersal for this species (Tunnicliffe 1981).

A combination of mathematical modeling and empirical measurements have also been used to study the physical environments of organisms (e.g., Monteith 1973; Gates 1980; Okubo 1980; Nowell and Jumars 1984; and Denny 1988). At the ecosystem level, such information is necessary to analyze the flux of various substances into and out of the components of a system (e.g., slowed currents limit nutrient supply in a kelp forest [Jackson and Winant 1983]; boundary layer hydrodynamics determine mass transport to and from benthic communities [Jumars and Nowell 1984]; turbulence affects the flux of nutrients driving phytoplankton productivity in the ocean [Lewis et al. 1986]). At the biogeographic

and community levels, analyses of fluid motions in the environment are sometimes necessary to understand the large- and small-scale spatial patterns of distribution of organisms that disperse by propagules such as wind-borne seeds or current-borne larvae (e.g., Scheltema 1975; Eckman 1983; Shanks 1985). Obviously the physics of water motion is also critical in producing patterns of distribution of phyto- and zooplankton (e.g., Denman and Powell 1984; Mackas, Denman, and Abbott 1985).

WHAT NEXT?

A number of directions for future research at the interface between organismal biology and ecology were discussed. Although our discussion ranged from everyone's favorite philosophies of science to each participant's pet research topic, I will attempt a concise summary.

Techniques for the Future

New techniques often pave the way for scientific progress, opening up problems that previously were not accessible to incisive research. Several empirical and theoretical tools were mentioned that may prove useful in the near future. On the empirical side, new molecular techniques that enable us to measure the genetic structure of field populations open exciting possibilities for investigating questions at the interface between population ecology and population genetics (as do the microbiological techniques mentioned above in the context of microcosm experiments). On the theoretical side, behavioral ecologists might borrow the models of irrational choice now being developed by economists (Tversky and Kahneman 1981). Artificial intelligence languages should be more useful than the more usual high-level computer languages for modeling the behavior of individuals aggregated into populations of interacting units. In the coming years there is likely to be extension of ESS and game theory modeling to include dynamical game theory (e.g., Brown and Vincent 1987). Similarly, relatively simple optimization models are giving way to more complex ones; work in dynamic optimization is one direction, and modeling that includes the effects of optimization under uncertainty is another (e.g., Mangel and Clark 1983, 1986, 1988).

Questions on Which to Focus in the Future

In spite of the temptation to find problems suited to the latest flashy technique, there was a consensus that we need to focus more deliberately on asking the right questions. We should let important unsolved biological problems, rather than

appealing research tools, be our guide for future research. While some partici-
pants stressed the importance of focusing future research on specific issues
important to mankind (such as the release of genetically engineered organisms,
spread of diseases, or destruction of ecosystems), others argued that the answers to
these practical problems, as well as to more basic academic questions, still hinge
on gaining a better understanding of what determines the abundance and dis-
tribution of organisms. It appears that a multiplicity of approaches is in order.

POPULATION REGULATION

One critical area for future investigation remains the problem of what factors
regulate populations. Rather than focus on resources, as we have tended to do in
the past, we should be more explicit about the demographic consequences of
behavioral, physiological, and biophysical mechanisms that affect survivorship
and reproduction, and that determine the distribution of individuals among
habitats.

WORLD DOMINANCE BY CERTAIN ORGANISMS

An interesting phenomenon, well known to biogeographers, is that there are
certain groups of organisms that arise (sometimes rather quickly) in the geo-
logical record and literally sweep the world. This is an ecologically important
phenomenon because such organisms tend to wipe out certain pre-existing
groups but to co-exist with others, for reasons we do not yet understand. What
are the general traits, if any, that contribute to world dominance by certain groups
of organisms?

VARIABILITY

A number of the directions of future research that we discussed share the
common theme of incorporating variability (within a population, within a hab-
itat, or of an individual) into ecological models. In analyzing ecosystems, commu-
nities, or populations, when should we retain the diversity of species or indi-
viduals, and when can we simplify?

It is crucial to recognize that the average dynamical behavior of a nonlinear
system can be very different from the dynamical behavior of the average (e.g.,
May 1986). Therefore individual differences can be quite important, and orga-
nismal-level information about the degree of variability within a population (or
species or community) will become increasingly necessary.

Not only should we pay more attention to how population dynamics are
affected by individual variability, but we should also investigate mechanisms
(such as those resulting from breeding systems or environmental heterogeneity)
that maintain variability in populations. Optimization models predict a "best"
phenotype for a habitat, and hence cannot account for the variation seen within a
population (or between different species utilizing the same habitat) (e.g., Gross,

chapter 1). In the future, such models should take into account environmental variations in space and time to explore the relationship between genetic variability and the predictability of particular habitat types. A compendium of the sorts of mathematical models that could lead to maintenance of variation would be very useful at this time.

Habitat variability in space and time is also a central feature of several other directions of future research. For example, when modeling the population dynamics of plants or sessile animals, we need to learn whether predictions can be made without detailed knowledge of the neighborhood (biotic and abiotic) around individuals. In addition, we should explore the extent to which the local population abundance of motile or sessile organisms is determined by characteristics of the resources available on a site versus characteristics of the mosaic of habitats in which the site is embedded (e.g., Pulliam, chapter 2). Future research should also explore factors that produce and maintain the spatial structure of populations in variable environments. Although dispersal (by seeds, larvae, or motile individuals) in patchy environments is no doubt a crucial factor in determining population dynamics (e.g., Roughgarden and Iwasa 1986) and is an important feature of life-history strategies (e.g., Jackson and Strathmann 1981), we should recognize the tremendous technical challenge posed by empirically studying this phenomenon in nature.

Variability within one individual (both phenotypic plasticity and learned behavioral change) represents another important topic for future research. What are the laws, if any, governing the relationship between phenotypic plasticity and genotypic variability in natural populations (e.g., Travis and Mueller, chapter 7)? How might genotype-environment interactions affect plasticity (e.g., Via and Lande 1985)? Some kinds of animals and some types of behaviors are modified by experience (learning) and others are not. Does the time-course of environmental events relate to this difference in flexibility? Dynamic game theories that consider mixed strategies versus coalition strategies or pure strategies might be employed to tell us those circumstances under which an individual ought to be flexible versus rigid in its behavior. At present such models are deterministic (e.g., Brown and Vincent 1987); the role of stochastic events might be incorporated in the future. Another aspect of variability within individuals that should be explored is the population-level consequences of such plasticity in behavior, morphology, or physiology. For example, in considering ESS models, is the effect of each individual doing particular behaviors with a certain probability the same as the effect of a population composed of certain proportions of individuals that each specialize in one behavior?

OPTIMIZATION MODELS

A good deal of attention has been paid by theorists to organisms as entities that behave according to some sort of "optimality." One problem with this approach has been the difficulty of determining what is being optimized. For example,

when considering optimal foraging, detailed questions of nutrition must be dealt with rather than simple caloric intake. Another problem with the optimality approach has been elucidating the constraints that limit the optimization process: for both plants and animals, we need a systematic exploration of the way in which physiology and physics constrain optimization.

An important direction for future research is to seek organizing principles of communities that are predictable from a knowledge of the degree to which behavior is optimized as a function of the density of a population.

PLANT ECOLOGY

Several specific areas of future research were mentioned for plant ecology. One is the coupling of multiple environmental factors as they affect an individual's performance. Once such coupling is better understood, we can move on to a more unified quantitative theory that can be related to models of plant geographic distribution or community composition.

Another area of future activity in plant ecology concerns the allocation of resources within individuals (e.g., Bloom et al. 1985). Analysis of the control of root-shoot allocation by plants in various environmental complexes should provide us with one simple pattern we can use to address questions at several levels of organization, from individual growth to competition and succession. Future modeling efforts should incorporate the roles of storage and of reproduction in mediating such allocation patterns. We should also explore the population- and community-level consequences of patterns of carbon and nitrogen allocation by plants into various products and defensive chemicals in different types of habitats.

Interface between Ecology and Evolution

Basic evolutionary processes shape the properties of individuals, which add up to the dynamical properties of populations. For too long, organismal biologists have tended to focus on the relationship between individual performance and evolution, while ecologists have tended to focus on the dynamics of populations without asking how the behavior of individuals affects population parameters. An overarching direction for future research should be the explicit relationships between individual performance and population dynamics. We must deal with the genetics as well as the behavior of populations if we are to understand how individuals determine the ways in which populations respond to change.

CONCLUSIONS

There appears to be a growing recognition that processes that occur at the level of individuals can form the basis for constructing a theoretical framework with which to interpret the properties of populations or communities.

Biological problems, rather than research techniques, should drive the directions of future investigations at this interface between ecology and organismal biology. There is considerable room for theoretical work of a great variety of kinds (ranging from simple phenomenological models to complicated mechanistic ones), as well as for empirical work of various sorts (ranging from insightful natural-history observations to manipulative field and laboratory experiments). If we are to make headway in this field, it is important to enhance communication between theorists and empiricists, and between ecologists, population geneticists, and organismal biologists.

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