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Ecological Experiments

Scale, Phenomenology, Mechanism, and the Illusion of Generality

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In attempting to understand the distribution and abundance of organisms, ecologists often seek general organizing principles to aid in understanding and predicting the responses of populations to environmental variation. The principle goal of this essay is to clarify the concept of generality in ecology. We are motivated by the perception that many ecologists attempt to generalize both theory and experimental results beyond specific experimental systems. In some cases, this generalization may be justified; in others, it is not. We believe that ecology as a science will benefit from an open discussion regarding the nature of and limits to generality. To this end, we (1) discuss the nature of ecological processes and their implications for epistemology and generality; (2) discuss concepts of generality and provide a mechanism-based definition; (3) offer a definition and several examples of mechanism, a concept that is central to generality; and, finally, (4) illustrate our position with a discussion of the role of mechanisms in ecological inquiry and with several examples. We emphasize at the outset that our discussions of specific research programs are meant solely to foster constructive discussion of issues related to generality in ecology.

The Nature of Ecological Processes

In the process of studies directed at providing an objective basis for understanding patterns in the distribution and abundance of organisms, ecologists have established three principles. First, the fundamental unit of ecology is the individual organism. Second, most ecological patterns result from multiple simultaneously acting processes (i.e., multiple causality). Third, very few generalizations apply to all ecological systems and remain valid regardless of spatial, temporal, and organismal scales. In the following, we discuss each of these principles and their implications for the process of ecological inquiry.

All ecological processes are ultimately transduced through individual organisms. Regardless of the scale that ecologists use to study ecological processes, these processes result from energy and mass exchanges among individual organisms or between individuals and the physical environment. Therefore, the fundamental unit of ecology is the individual organism and every individual is potentially unique. The uniqueness of individuals results from the nature of inheritance and from the fact that each individual has a unique history of interaction with its environment (including other organisms) throughout its life. The uniqueness of individuals means that individual organisms cannot necessarily be aggregated in ecological theory by imposition of the law of large numbers or by the assertion that individuals can be treated as if the differences among them are inconsequential. Nonetheless, the vast majority of models in population biology are based on this assertion. We submit that this is a dangerous assertion because the fundamental units of ecology do not comprise homogenous sets. It may be the case that for certain questions, particularly those that involve spatial or temporal patterns on large scales, this assumption may be safely made. However, the validity of imposing such an assumption should be tested before the assumption is made.

Most, if not all, of the patterns that ecologists seek to explain result from several, if not many, simultaneously acting and potentially interacting processes (Quinn and Dunham 1983). Thus, ecological patterns are complex, and that complexity should be reflected in both theory and empiricism. Because multiple interacting causal mechanisms may often produce the patterns that ecologists seek to understand, the potential for multiple causal mechanisms must be incorporated into the construction of ecological theory and into the design of ecological experiments.

Ecologists have also established that very few general principles apply to all ecological systems and remain valid irrespective of spatial, temporal, or organismal scales. Examples of such general principles are the first and second laws of thermodynamics (the law of conservation of energy and the law that conversion efficiency among energy forms must be less than 100%, respectively). Energy and mass balance must hold in all ecological systems regardless of the system boundary. However, most processes or principles that ecologists use to understand the patterns they study are not general because they are valid only over a restricted range of spatial, temporal, or organismal scales (= the domain of generality of a given process or principle). The domain of generality of a given process is process-specific.

The preceding considerations have at least two important implications for ecology: in the design of ecological experiments and in the generalization of experimental results. The first implication is that ecological theory cannot generally be done in a manner that ignores the differences among individuals. The second implication is that because multiple interacting causal mechanisms often produce the patterns that ecologists seek to understand, the potential for multiple causal mechanisms should be incorporated into the construction of ecological theory and into the design of ecological experiments.

The Concept of Generality and the Importance of Mechanism

When ecological theory is constructed such that differences among individuals are ignored or assumed negligible and/or such that a single mechanism is assumed to produce a particular pattern, a coarse and usually unrealistic body of theory (e.g., the large literature on Lotka-Volterra dynamics in community ecology) is the result. Many ecologists refer to such simple, unstructured theory as "general," but in reality these theoretical constructs often lack logical generality and are best described as extremely simple and crude. A general theory is one that has many special cases and holds true for all of them, not one that fails to hold for any special case even though it may capture a few gross features. The recent increase in the use of physiologically structured, individual-based models (e.g., Adams and DeAngelis 1987, DeAngelis and Gross 1992, DeAngelis et al. 1993, Dunham 1993, Dunham and Overall 1994) in population biology probably reflects the realization that the preceding implications are important.

Several ecologists (e.g., Foster 1990, Hurlburt 1984, Underwood 1986, Underwood and Fairweather 1986) have suggested that part of the difficulty in understanding patterns in ecology arises because much of the evidence that supports putative causal mechanisms is poor. In part, this is because single-factor causality is often assumed and methods and experimental designs used in many studies do not adequately explore alternative hypotheses that involve the potential effects of multiple interacting mechanisms. In addition, the patterns themselves are often not well documented. For example, Foster (1990) examined patterns of zonation in intertidal macroalgal assemblages and noted that most research done on these assemblages had been conducted at a few protected sites where patterns of zonation are distinct. Foster surveyed a variety of algal assemblages at wave-exposed sites and demonstrated considerable variation in assemblage structure. Foster argues convincingly that explanations (e.g., mussel–algal interactions) for zonation in macroalgal assemblages developed at only a few sites may be inadequate to explain patterns in macroalgal assemblages at all or even most sites. Simply put, the commonly accepted causes of algal zonation may not apply generally due to environmental heterogeneity. We suggest that the problems described by Foster (1990) are more pervasive in ecology than is commonly appreciated. Ecology needs a set of objective criteria for judging the domain of generality of theory and of the results of experiments designed to test theory.

Generality—A Definition

Foster provides one definition of generality applicable to the macroalgal assemblages he studied: "By generality, I mean over what proportion of the coast in some defined geographic region does a particular organization apply" (1990: 22). This definition is in the right spirit, but we suggest the following alternative definition: *By generality we mean the range of spatial, temporal, and organismal scales over which a particular mechanism or set of mechanisms applies.* This definition differs from Foster's in two important respects. First though different ecological mechanisms and processes may operate over different temporal, spatial, and organismal scales, Foster's definition explicitly incorporates only the spatial scale, whereas our definition incorporates all relevant scales. Second, Foster's definition attempts to define generality in terms of ecological organization rather than the processes or mechanisms that produce patterns in ecological organization, whereas our definition, since it is clear that, similar patterns of community organizations may be produced by different mechanisms, is in terms of the set of temporal, spatial, and organismal scales over which the mechanisms that produce a particular pattern in nature are valid.

Mechanism—A Definition

In order to infer the domain of generality of a particular causal explanation for an ecological pattern, we must be explicit about what we mean by *mechanism*. There is some disagreement among ecologists with regard to the meaning of mechanism (e.g., Peters 1991, Schoener 1986). *By* mechanism *we mean an appropriate level of reductionism that provides a causal explanation of the functional relationship among a set of variables.* In discussions of mechanism with our colleagues we have heard the argument that "one person's mechanism is another's phenomenological description" in many forms. Note that by our definition, the relationship between pattern and mechanism is scale-dependent and hierarchical in nature. The key in this distinction is the determination of what the "appropriate level of reductionism" is in any attempt to understand a particular ecological pattern. For a particular set of functional relationships to qualify as a mechanism to explain a particular pattern, the functional relationships must be quantified independently of the pattern of interest and at a lower level of hierarchy. We clarify the hierarchical nature of the relationship between pattern and mechanism by example in the next section. Mechanisms are generally described by a set of parameters that allow prediction of the functional relationships among the variables of interest. This set of parameters is subject to the following constraints: (1) they cannot be derived from the variables under consideration and (2) they must be objective and measurable. The first constraint precludes regression models and other such models based solely on curve-fitting procedures (for example) from being mechanisms and stands in contrast to "instrumentalist" approaches to ecology (e.g., Peters 1991). The second constraint ensures that hypotheses that involve ecological mechanisms are empirically testable. The domain of generality of a particular mechanism or set of mechanisms is simply the range of temporal, spatial, and organismal scales over which the set of variables and the associated parameter set remain invariant.

Mechanism—An Example

There is often disagreement among ecologists about the importance of mechanism, as well as about what constitutes a mechanism. To illustrate our definition of mechanism as a level of reductionism subject to the above constraints we provide the following example from physiological ecology. The set of complex mechanistic interactions that describe the mass and thermal energy exchanges between an individual organism and its environment are well-known and have been described in detail elsewhere (e.g., Dunham et al. 1989, Gates 1980, Porter and Gates 1969, Porter and Tracy 1983). This set of interactions can be summarized by a set of coupled thermal energy–mass balance equations (Porter and Tracy 1983). A simplified version of these equations is shown in Figure 2-1. The set of interactions which result in the rates of change of temperature and mass of an individual organism at any particular time and which are described by the set of equations depicted in Figure 2-1 constitutes an ecological mechanism. This mechanism is general in that it applies on any spatial and temporal scales relevant to an individual organism and can be applied to any individual organism irrespective of the type of organism or environment. In order to apply this mechanism to a particular organism, a number of physical characteristics and functional relationships characteristic

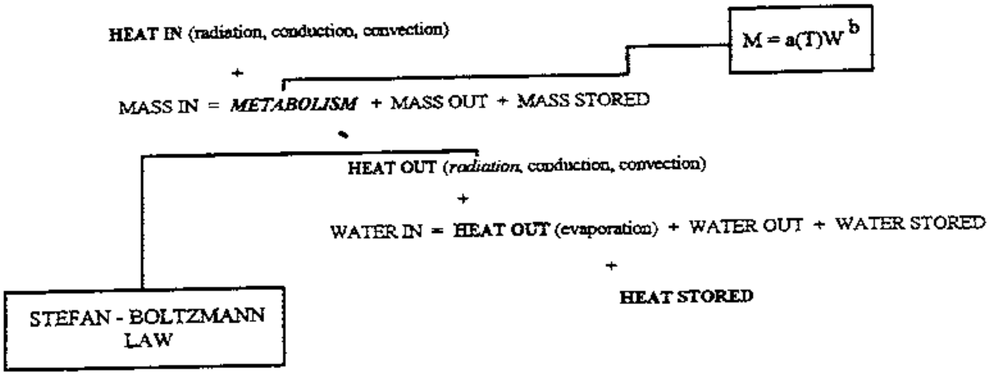

Figure 2-1. Simplified version of the coupled heat and mass balance equations relating variation in operating environments to body temperature and net allocatable resources. Modified from Dunham (1993), Dunham et al. (1989), and Porter and Tracy (1983).

of the organism must be supplied. For illustrative purposes, we examine two terms from this complex set of equations in detail (Fig. 2-1). The first term specifies the rate (Q_{IR}) of heat loss from the surface of the organism due to infrared radiation. The physical relationship that describes the rate of heat loss due to emission of infrared radiation is known as the Stefan-Boltzmann law and may be written $Q_{IR} = \sigma\varepsilon K^4$, where Q_{IR} is the rate of heat loss due to infrared radiation (Watts), σ is the Stefan-Boltzmann constant (5.67×10^{-8} Watts$\cdot$m$^{-2}\cdot K^{-4}$), ε is the emissivity of the organism's surface in the infrared wavelengths (dimensionless), and K is the surface temperature of the organism (° K) (equation 1).

The second term describes the dependence of heat produced by metabolism on body temperature of the organism and on the organism's mass. For a small ectothermic vertebrate this relationship may be written $M = a(T_b)W^b$, where M is the rate of heat production due to metabolism (Watts), T_b is body temperature (°C), a is a function of T_b, and b is a fitted constant (equation 2). Note that the relationship described by equation 2 involves a fitted function (a which depends on T_b and a fitted constant (b) and that the relationship described by equation 1 involves a measured quantity (ε). The fitted function, fitted constant, and measured quantity render the mechanism embodied by the set of thermal–mass balance equations (Fig. 2-1) specific to the organism under consideration. However, this does not affect the generality of the thermal–mass balance equations as a mechanism responsible for the rates of change of temperature and mass of any particular individual in any environment.

Physics and physiology dictate the terms and form of the thermal–mass balance mechanism, and those are general irrespective of the type of organism or environment. In contrast, consider the term describing the dependence of the heat produced by metabolism on the body temperature of the organism and the organism's mass. Equation 2 describes the form of this relationship for a small ectothermic vertebrate, but the fitted function, $a(T_b)$, and constant, b, represent empirical fits to laboratory data. The empirically estimated function, $a(T_b)$, and constant, b, and the estimate of metabolic heat production provided by equation 2 constitute an acceptable estimate of the appropriate term in the set of thermal–mass balance equations. However, equation 2 provides no information about the actual physiological mechanism that relates body temperature and mass to metabolic heat production because the parameter estimates are derived empirically by a curve-fitting procedure from data on the response variable M taken at different levels of the experimental variables T_b and W. Note that the empirically derived relationship between M and the fitted function $[a(T_b)]$ and estimated parameter (b) can serve as a component of the mechanism described by the coupled mass–energy balance equations. However, the same relationship by our definition cannot be a mechanism of metabolic heat production because, at this level of hierarchy, the estimated parameters are derived from the variables of interest. As a consequence of the specificity of the relationship between M, $a(T_b)$, and b, the domain of generality associated with equation 2 is precisely the organism and ranges of the values of the experimental variables used in the experiment to relate measurements of M to experimentally controlled values of T_b and W.

Mechanism—A Practical Example

We provide an explicit example that illustrates the importance of mechanism in developing hypotheses about the causes of an ecological pattern in a system potentially involving multiple interacting causes. There is an interesting and perplexing pattern of geographic variation in several life history characters among three populations of the canyon lizard (*Sceloporus merriami*) that occur along a steep elevational gradient in Big Bend National Park, Texas (Dunham et al. 1989; Grant and Dunham 1988, 1990). These populations are Maple Canyon (MC, 1609-m elevation), Grapevine Hills (GV, 1036 m), and Boquillas Canyon (BQ, 560 m). The pattern of variation in life history characteristics and the environmental differences among these sites are discussed in detail by Dunham et al. (1989) and Grant and Dunham (1990). For the purposes of this example, we consider only the differences among these populations with regard to individual growth rates of yearling lizards (Fig. 2-2a). The pattern of geographic variation in individual growth rates for other age classes is similar and is discussed in detail elsewhere (Dunham et al. 1989, Grant and Dunham 1990). The perplexing aspect of the pattern of among-population variation in individual growth rates is that individuals from the population at the intermediate elevation (GV) have higher average growth rates than do individuals from either the low-(BQ) or high-(MC) elevation population. Within the GV population, individual growth rates depend on food resource availability such that individual growth rates are higher during periods of high resource abundance (Dunham 1978). Several environmental gradients that operate in this system potentially influence individual growth rates. In this system, both primary productivity and associated prey availability depend on rainfall and, because precipitation increases with elevation, prey availability also increases with elevation (Fig. 2-2b) (Dunham 1993, Dunham and Overall 1994, Dunham et al. 1989, Grant and Dunham 1990). Biophysically imposed thermal constraints limit the amount of time an individual can be out of refugia (crevices, etc.), and foraging on each day throughout the active season and the fraction of the day during which an individual lizard can forage increases with elevation (Fig. 2-2b) (Grant and Dunham 1990). These considerations lead to the prediction that there should be a pattern in which individual growth rates increase monotonically from the low-elevation population (BQ) to the high-elevation population (MC) because food

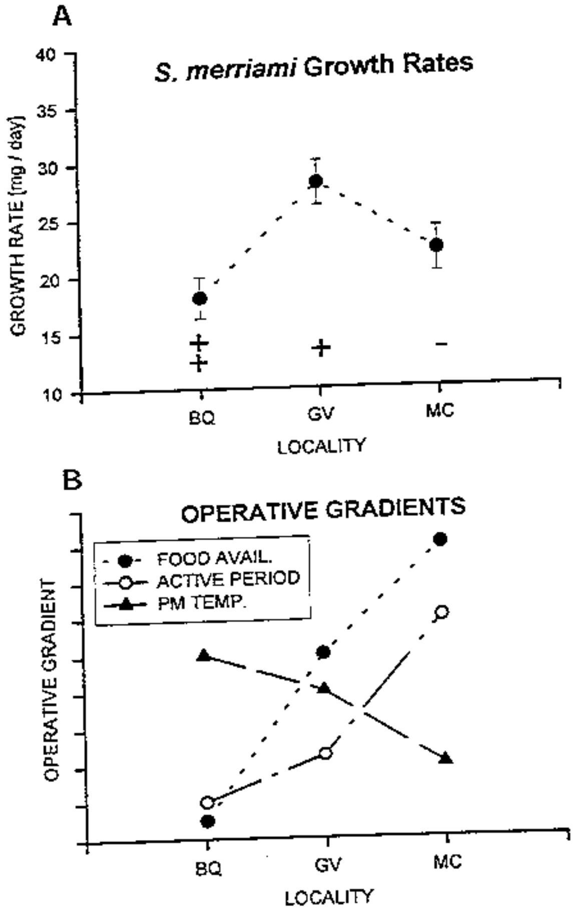

Figure 2-2. (**A**) Pattern of geographic variation in individual growth rates of yearlings among three populations of the lizard *Sceloporus merriami*. (**B**) Pattern of variation in three environmental gradients (food availability, length of daily activity period, and average operative temperature, (T_e) during scotophase among three populations of the lizard *S. merriami* from Big Bend National Park, Texas. BQ is the Boquillas Canyon population (elevation 560 m); GV is the Grapevine Hills population (elevation 1036 m); and MC is the Maple Canyon population (elevation 1609 m).

availability and time available for foraging are lowest at low elevations and increase monotonically with elevation (Fig. 2-2b). Clearly, this prediction is not met and some other set of factors must be involved.

Growth rate can be limited by any mechanism whereby the amount of assimilated resources available for allocation to growth is limited. In the present system, such limitation can occur in two different ways: (1) the rate of prey ingestion is limited by availability of prey and/or time during which foraging can occur, and (2) the rate at which ingested prey can be digested and the resulting nutrient resources assimilated is limited by the nature of digestive physiology (Beaupre and Dunham 1995, Beaupre et al. 1993, Dunham et al. 1989). The second mechanism is termed *process limitation* (Dunham et al. 1989). In *S. merriami*, as in other ectotherms, digestive physiology is strongly temperature-dependent (Beaupre and Dunham 1995, Beaupre et al. 1993). At naturally occurring temperatures in these populations, passage rates are such that much of the digestion of prey items ingested during the day takes place at night, when these lizards are normally in refugia (Beaupre and Dunham 1995, Beaupre et al. 1993). There is significant variation among these populations in the average operative environmental temperatures available to these lizards such that at any particular time of day the average temperature declines with increasing elevation (Fig. 2-2b) (Dunham et al. 1989, Grant and Dunham 1990). Metabolizable energy (ME) and passage time are two temperature-dependent variables that influence the rate at which ingested food is digested and assimilated (Beaupre and Dunham 1995, Beaupre et al. 1993). Metabolizable energy is a measure of the amount of the energy ingested that is assimilated and available for allocation to processes such as growth. Passage time is a measure of the amount of time it takes the digestive tract to completely process ingested food. In *S. merriami*, for a given meal size, ME decreases significantly with increasing temperature (largely due to increasing uric acid production) over the range of temperatures normally exhibited by field-active lizards (Beaupre and Dunham 1995, Beaupre et al. 1993). In *S. merriami*, passage time decreases significantly with decreasing temperature over the range of temperatures normally exhibited by field-active lizards (Beaupre et al. 1993). In addition, rate of food consumption by *S. merriami* decreases significantly with decreasing temperature over the range of temperatures normally exhibited by field-active lizards (Beaupre et al. 1993).

The interaction among the thermal dependence of ME, passage time, and consumption rate, and the environmentally imposed temperature gradient (Fig. 2-2b) suggests a mechanistic hypothesis for the lower growth rate of individuals in the high-elevation (MC) population. That is, lower individual growth rates in the MC population may result from process limitation in which the resources assimilated per unit time that could be allocated to growth are reduced relative to the GV population because of decreased passage time and consumption rate due to the lower temperatures at which digestion must take place in the MC population. The lower individual growth rates seen in the BQ population relative to the GV population are hypothesized to be due to lower prey availability due to lower rainfall and resulting primary productivity interacting with a biophysically imposed constraint that greatly reduces the time available for foraging in the BQ population. Thus, the overall hypothesis that explains the pattern of geographic variation in individual growth rates in this system involves multiple interacting mechanisms (process limitation due to complex nonlinear temperature dependencies of digestive performance and resource limitation due to lower prey availability and biophysically imposed thermal constraints on time available for foraging) and interactions among several environmental gradients (temperature, precipitation, productivity, and food availability). This complex causal scenario can be tested experimentally in several ways. The most obvious approach involves a resource supplementation experiment in which prey availability is artificially increased in all populations. Under the current causal hypothesis, a strong positive growth rate response is predicted in the BQ population, a smaller response in the GV population, and no increase in growth rate in response to increased prey availability in the MC population.

Mechanism in Ecological Experiments

Currently most ecological experiments are not formulated and carried out with explicit mechanisms as the alternative hypotheses being tested. That is, most ecological experiments are phenomenological or mechanism-vague (or mechanism-free). For example, most density manipulation experiments which test for a significant effect of the density of one species on some response variable (e.g., growth rate or density) of another species, when considered alone, provide no means for inferring the causal mechanism whereby a response to density manipulation is produced. Phenomenological experiments may be used to suggest hypotheses of causality but are rarely adequately designed to test potentially important alternative causal mechanisms or even the "mechanisms" that the experimenter claims to be testing. Typically, such mechanism-vague experiments: (a) involve mechanisms (in the sense defined previously) that are unspecified or unknown, (b) involve manipulated variables that bear no unambiguous relationship to a mechanism or set of mechanisms, and (c) produce outcomes that are not generalizable to other systems or even to the experimental system in which they are carried out when the range of experimental variables falls outside the range of manipulations already accomplished or when initial conditions vary. In such experiments, manipulated and response variables generally have no clear mechanistic connection and multiple interacting causes may be responsible for the observed response to experimental manipulation.

Statistical Considerations

The nature of experimental design and statistical analysis may pose problems for generalizing experimental results to natural systems. The purpose of doing an experiment is to test a statistical hypothesis. Basic principles of experimental design involve establishment of orthogonal contrasts among experimental variables. Establishment of orthogonal contrasts allows one to test hypotheses of main effects in factorial designs independently but may not reflect naturally occurring covariation among the experimental (= predictor) variables. For example, consider a two-factor analysis of variance with three levels of each factor (Fig. 2-3). Natural covariation between these two factors may be reflected in only a limited subset of treatment combinations. Suppose that, in nature, there is negative covariation between the magnitude of factor 1 and the magnitude of factor 2. In the example diagrammed in Figure 2-3, treatments where both factors are high or where both factors are low do not occur naturally. Most experimental designs currently employed by ecologists yield yes-no answers (there is or there is not a statistically significant effect of experimental variable x on response variable y). In a case such as that presented in Figure 2-3, significant treatment effects may be due to combinations of treatment levels that do not occur naturally. In addition, the results and interpretations of analysis of variance or similar linear model analyses are dependent on which predictive factors (treatments) are included in the experiment and, therefore, in the analysis. In such an analysis, the magnitude of the main effect of a

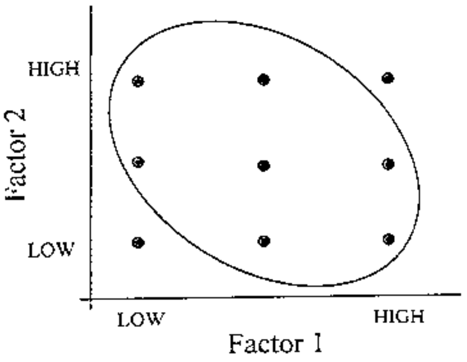

Figure 2-3. Diagram of a 3 × 3 factorial design ecological experiment. Assume that the ellipse encloses the treatment combinations that occur in nature. To the extent that significant treatment main effects or interaction effects are due to treatment combinations that never occur in nature (e.g., low-low or high-high combinations), extrapolation of the results of such experiments to natural systems is problematic.

factor (e.g., density of another species) may be large in a controlled experiment, yet if the effect is reanalyzed in the presence of other factors (e.g., variation in the biophysical environment) statistical significance may be lost or the magnitude of the effect may change dramatically. As a result of these two issues, it may often be impossible to understand the dynamic behavior of natural systems based on experimental results (for an example see Petraitis, this volume).

On the Relationships among Mechanism, Scale, and Generality

All studies in ecology begin with a specific phenomenon or set of phenomena that requires explanation (Fig. 2-4). It is usually the case that many potential mechanisms may be responsible for a given pattern. In order to understand a particular ecological pattern, one must identify the subset of potential mechanisms that is actually responsible for the pattern of interest. It is also the case that each potential mechanism may act over a unique set of scales. For example, population density may be limited by physiological constraints on reproduction (e.g., developmental rates, pelvic girdle size, etc.) which may be common to all members of a species. Alternatively, population densities may be limited by food availability or predation, both of which may vary among populations. Each potential mechanism, therefore, is valid over a set of spatial, temporal, and organismal scales. The set of scales over which a given mechanism (or set of mechanisms) is valid directly determines the appropriate spatial, temporal, and organismal scales for critical experimental tests of the mechanisms in question. Thus, as depicted in Figure 2-4, for any epistemological sufficient phenomena, potential mechanisms may be listed ($M_1, \ldots, M_n$ and critical experiments may be designed ($\text{EXP}_1, \ldots, \text{EXP}_n$) each with its own spatial, temporal, and organismal scale ($\text{SCALE}_1, \ldots, \text{SCALE}_n$). Execution of the designed experiments should lead, ultimately, to a subset of mechanisms (M^*) to which the original phenomenon is attributed. The set of mechanisms included in M^* collectively exhibits a unique set of spatial, temporal, and organismal scales. It is the relevant scales of M^* that determine the domain of generality over which the mechanisms in M^* have explanatory and predictive power. Thus, if M^* is known, an unambiguous statement regarding the generality of experimental results may be made.

Observation and Mechanism in Ecology, Illustration by Example

The fundamental question that concerns us is: How do we recognize the generality of a particular principle derived from observations taken in the context of ecological study? Using examples from the present volume and the primary literature, we illustrate in the following discussion how the concepts of mechanism and scale determine directly the domain of generality over which a given experimentally derived principle applies. Our choice of particular studies as examples is not meant as criticism; rather, we chose these examples because of their utility for illustrating epistemological limitations shared to a greater or lesser degree by all ecological studies. Prior to discussion of specific

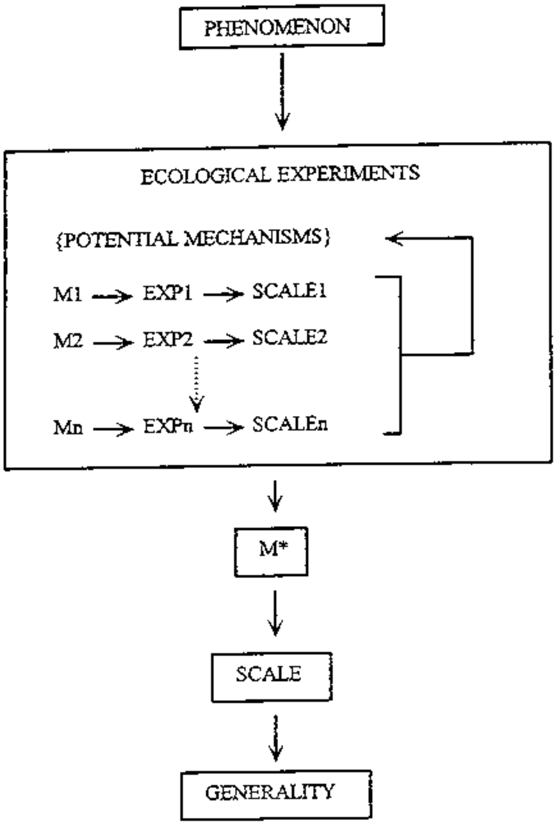

Figure 2-4. Relationships among mechanisms (alternative hypotheses of causality), mechanism-explicit ecological experiments, the spatial, temporal, and organismal scales of ecological experiments, and the domain of generality over which the results of experimental experiments apply.

examples, it is useful to consider the variety of contexts under which observations are made in ecological studies.

Observation is the fundamental tool of all scientists, and studies differ only in the degree to which the observer exerts control over the circumstances under which observations are made. In ecology, we define three broad classes of observation: (1) natural history; (2) mechanism-free (phenomenological) experiments, and (3) mechanism-explicit experiments. We note that these categories are not necessarily mutually exclusive—that is, it is possible to test critically some mechanisms with natural history (i.e., uncontrolled) observations, and the distinction between mechanism-free and mechanism-explicit experiments will depend to some extent on the level of reductionism implied by each hypothesis and associated experiment. Nevertheless, these distinctions are useful for illustrating the relationships among mechanism, scale, and generality.

The primary purpose of natural history is to observe and document patterns of variation in natural phenomena. The documentation of pattern in nature produces ecological questions at the most fundamental level, and it is toward answering these questions that the activities of ecologists are generally directed. At their core, natural history observations may establish pattern and often suggest a potentially broad range of mechanisms that may be responsible for an observed pattern. In some cases, competing or alternative mechanistic hypotheses may be tested through further uncontrolled observation of natural history. Natural history observations can falsify some mechanisms, but they generally cannot unambiguously support any particular mechanism as responsible for pattern in nature. Typically therefore, identification of relevant mechanisms cannot be accomplished without imposing greater control on conditions of observation. Thus, because exact mechanisms cannot be clearly established, the scale over which a particular pattern obtains and also its domain of generality remain ambiguous if only natural history observations are utilized.

In mechanism-free or mechanism-vague experiments, a manipulation is performed with the aim of testing a specific prediction. However, either a specific mechanism is not stated or more than one mechanism (usually unspecified) may produce the predicted result. Investigators focus on particular factors without a clear statement of the hypothesized relationship(s) between manipulated independent and observed dependent measures. For example, many studies have manipulated densities of potential competitors to study "competition" or predation. Competition, as used in this sense, is actually a family of mechanisms, including potentially a variety of inter-and intraspecific interactions (e.g., competition for food, interference, and a host of corollary effects attendant to changes in species density). Careful attention to experimental detail is required to differentiate among the variety of mechanisms embodied in "competition." Without knowledge of the exact mechanisms that produce an experimental result, it is difficult to determine the scale over which the result may obtain in nature, and thus it is impossible to specify the domain of generality of the principle being tested. That mechanism-free experiments are impossible to generalize does not necessarily diminish their utility. Mechanism-free experiments play a critical role in refining hypotheses and in suggesting potential mechanisms for further, more controlled, studies.

Mechanism-explicit experiments are among those that are most tightly controlled. The experimenter has identified a single or very few mechanisms and has carefully designed the experiment to test critically the mechanisms of interest as hypotheses to account for some observed behavior. Mechanism-explicit experiments have the greatest potential for unambiguously identifying mechanisms responsible for a particular pattern. Tightly controlled experiments designed to test particular mechanisms give the experimenter confidence that the tested mechanism or set of interacting mechanisms (if not falsified) is responsible for pattern in nature. Once appropriate mechanisms are identified, the scale over which each mechanism operates can be inferred, and an explicit statement concerning the domain of generality of the principle being tested may be made. For example, suppose an experimenter determines that two species compete with each other through direct interference of one of the species with the other. Interference competition operates on the spatial scale determined by the amount of space required for one individual of each species to interact and on the temporal scale which determines how often individuals of these two species will occur in syntopy. The domain of generality over which interference competition is likely to influence population dynamics of the species in question is, therefore, all populations of these species that occur in syntopy and that exhibit interference behavior.

We emphasize here that it is not our intention to assign greater or lesser value to any of the three observational contexts we have identified. Clearly, the advancement of ecology as a science requires all three kinds of observation. We maintain only that a concise statement of the generality of a particular experimental result hinges on a clear understanding of the mechanism(s) responsible for that result. In our opinion, only mechanism-explicit experiments can provide the required level of understanding for unambiguous generalization. Our arguments have implications for the interpretation of experimental results and may aid in determining the degree to which particular experimental results are generalizable. In the remainder of this essay, we illustrate the relationships among mechanism, scale, and generality with specific examples.

Studies of Ectotherms in Big Bend

The mechanistic explanation of geographic variation in life history has been the focus of our research on ectothermic vertebrates in the Big Bend region of Texas. Both *S. merriami* (as just described) and the mottled rock rattlesnake (*Crotalus lepidus*) exhibit similar variation in growth and size along an elevational gradient (Beaupre 1995a, Grant and Dunham 1990). Our approach has been to quantify the relevant fluxes of mass and energy through individuals by quantifying interactions between the properties of organisms (physiological and behavioral) and their environment (thermal distributions, seasonality, and productivity). Our goal in each case is to narrow the set of potential mechanisms $(M_1, \ldots, M_n)$ by (1) making critical observations in nature that can falsify some mechanisms and (2) designing critical experiments to test those mechanisms that cannot be falsified by observation. As such, the process is iterative, and it is our hope to eventually understand the natural complexity of these systems at a mechanistic level.

We are the first to acknowledge that we are far from a complete mechanistic understanding of environmental effects on life history. However, our studies have documented complex trade-offs among a number of mechanisms that affect the patterns of interest. For example, variation in metabolism, growth rate, and adult body size of *C. lepidus* on an elevational gradient may be the complex result of simultaneous variation in environmental thermal distributions (that affect body temperature); prey capture success, which varies with productivity; and time available for foraging (Beaupre 1993, 1995a, b, 1996). We have already described such complex and interacting effects on growth and size of *S. merriami* (see above). These processes qualify as mechanisms by our definition, because they operate at a lower level of hierarchy (individuals) than the patterns we wish to explain (populations). As the set of mechanisms and their likely interaction is narrowed, specific experimental tests of mechanistic hypotheses can be designed. An example of such a test is the supplemental feeding experiment proposed here for *S. merriami*. Through the iterative process of observation and experimentation, each employed as appropriate, we hope to attribute much of the variation in this system to sets of interacting mechanisms (M^*). Understanding these mechanisms will allow an unambiguous statement regarding the domain of generality (on organismal, temporal, and spatial scales) of the processes that we study. We are not to the point of making such an unambiguous statement, and we are aware of the implications for generalization posed by the complexity of our systems.

Mechanism, Higher Order Effects, and Higher Order Interactions Recently there has been a great deal of concern over the existence and interpretation of higher order effects and higher order interactions in ecological systems and associated experiments (e.g., Abrams 1983; Adler and Morris 1994; Billick and Case 1994; Fairweather 1990;

Wootton 1993, 1994). This concern is motivated by the following question: To what extent can the complex dynamics of communities and ecosystems be predicted with knowledge of pairwise species interactions? Clearly, this question cannot be addressed with only experimental data on pairwise interactions because the experiments and data are at the wrong scale to address the fundamental issue. For illustrative purposes we consider the typical approach to answering this question. Typically, investigators conduct a set of pairwise and generally mechanism-free experiments and then model the resulting pairwise interactions using simple mathematical constructs like ordinary differential equations or difference equations. The next step is constructing a larger model that combines the previously derived pairwise models in additive fashion and makes some predictions about the dynamics of the complete system based on simple pairwise interactions. This set of predictions is then compared to data from an experiment that involves all relevant species. The comparison of model-based prediction with experimental results can only have two outcomes: either there is agreement between the predictions of the model and the results of the experiment or there is no agreement. A lack of agreement may occur for many reasons, including: (a) error in the data, (b) incorrect pairwise or additive models, (c) indirect effects that must be modeled at a finer scale, and (d) nonlinear "higher order" effects that cannot be predicted by simple linear combinations of pairwise interactions. The indirect effects mentioned in (c) are effects of one species on another mediated through a third species. This kind of interaction is easily incorporated into simple models because it occurs by the only "mechanism" normally incorporated into such models (numbers of organisms of each type, experimentally estimated rates of increase, and interaction coefficients). As an example of the "higher order" effects described in (d), consider a situation where, say, species A influences the number of refugia available to species B by eating macrophytes and species B has fewer places to hide from species C, which consequently eats disproportionately more of species B than it would if species A were not present. Wootton (1993, 1994) and others would argue that this kind of effect could not be predicted based on pairwise comparison and that experiments that involved all three species would be required to elucidate the "higher order" term that describes this interaction. Although we agree for the comparison involving these relatively simple experimental systems and models, a critical issue is being overlooked that is fundamental to issues of scale, mechanism, and generality in ecology. The distinction that Wootton and others raise between indirect effects and higher order effects is artificial because it arises solely due to the inadequacy of the original model with respect to mechanism. These models are generally implemented using empirically derived relationships among numbers of organisms of each type, experimentally estimated rates of increase, and experimentally estimated interaction coefficients which attempt to incorporate density dependence. Note that these empirically derived relationships are not mechanisms under our definition because they are derived by a curve-fitting procedure from variables at the same level of organization as the pattern they are attempting to explain. It is simple to incorporate interactions that act directly on numbers of organisms into these models because the indirect effect can be expressed directly in terms of the currency of the model numbers of each species. In the preceding example of a "higher order" effect, an investigator that considers only change in numbers of each species will not be able to explain the disproportionate decrease in species B. However, it seems reasonable that careful attention to mechanism (as we define it) in this system might lead to the realization that the supposedly ''nonlinear'' effect was actually the complex result of several interacting linear effects. For example, species A causes a linear decrease in macrophyte density with the result that refugia eventually become limiting, and there is a linear increase in the number of species B exposed to predation with a concomitant linear increase in the number of species B captured by species C. This chain of causality could occur with no change in the density of species A. Such a simple causal scenario could explain what would look like a complex nonlinear interaction, as the result of a series of interacting linear functions. In this case, as with most of the debate over higher order effects and higher order interactions, the lack of mechanism results in an inability to generalize to more realistic cases. Thus, we believe that much of the argument over higher order interactions derives from (1) failure to explicitly incorporate mechanism into theory and (2) attempts to generalize the results of mechanism-free experiments.

Experimental Exclosures Competition among guilds of seed-eating rodents in the Chihuahuan desert has been the subject of long-term studies involving experimental exclosures (Brown, this volume, Brown and Munger 1985, Brown et al. 1986, Heske et al. 1994). Brown and coworkers have fostered a paradigm in ecological field studies. Their experiments have documented increases in population density of small granivorous rodents in response to removal and exclusion of large granivorous rodents of the genus *Dipodomys*. These density increases of small granivores have been attributed to competitive release. The pattern of increase in granivores is consistent with the hypothesis of some generalized competitive release. However, the exact mechanisms (interference, exploitation, etc.) that govern the response remain unknown. It is also the case that the experimental manipulations may not rule out some alternative explanations. For example, *Dipodomys* ssp. were excluded from experimental plots by gates which are too small to allow free movement of kangaroo rats. Such gates are also likely to restrict free movement of large viperid snakes that may consume many rodents on an annual basis. Heske et al. (1994) attribute immediate increases in granivore density on *Dipodomys* removal plots to migration of granivores from surrounding areas and active selection of *Dipodomys*-free microhabitats. Are migrating granivorous rodents responding to decreased density of *Dipodomys* or to decreased density of snake predators? Heske et al. (1994) note that insectivorous rodents (genus *Onychomys*) show no response to *Dipodomys* removal and argue that this observation supports the competitive release hypothesis rather than a decrease in predators. However, alternative explanations may exist for the failure of *Onychomys* to respond (e.g., insectivorous rodents may differ in their behavior and in their propensity to move among sites).

These considerations suggest that the *Dipodomys* exclusion experiments are mechanism-free or mechanism-ambiguous experiments. We note that ambiguity of mechanism is largely due to the laudable attempt to produce realism in these experiments. Nevertheless, ambiguous mechanisms lead to an inability to specify the conditions under which a given experimental result will be repeated, and thus it is impossible to specify the domain of generality of the principles of competition tested by these experiments. For example, based on the Chihuahuan desert experiments, what would we predict as the outcome of a similar manipulation in the Sonoran desert? Clearly, any prediction would be based on previously observed pattern, rather than on an explicit mechanistic theory of interaction for the species present in the new system.

Experimental Communities Lawler and Morin (1993) constructed food chains of protists in microcosms to study how the population dynamics of these protists varied with food chain length and with the presence or absence of omnivorous top predators. Their approach was motivated by the desire to test the predictions of a vast volume of virtually data-free food web theory. Lawler and Morin chose simple and manipulable systems in an effort to match the assumptions of theory to as great a degree as possible.

In their manipulations, food chain elements consisted of an initially similar assemblage of bacteria to serve as prey, two types of bacterivorous ciliates, an omnivore that could persist on either bacteria alone or on bacteria and a bacterivorous ciliate, and a top predator that would eat only ciliates. Their primary manipulations were food chain long (three elements) or food chain short (two elements) and omnivore present or absent. They measured two variables as indicators of system stability: time course of abundance and variance in abundance. Lawler and Morin's results supported the notion that population fluctuations and extinctions will increase with increasing food chain length and that predators feeding on multiple prey species are better buffered from system fluctuations than are specialists. These results were in general agreement with expectations from food web theory.

Lawler and Morin achieved their stated goals and were duly cautious in generalizing their experimental results. They offer the following thoughts in their closing paragraph (Lawler and Morin 1993:682): "Convincing statements about the generality of these patterns will require examination of many more species assembled in various trophic combinations." This quote reflects a pervasive and popular view of generality that is based on the notion that general principles are those that apply to the majority of cases. The show-of-hands concept of generality is also at the core of the meta-analysis approach (Gurevitch et al. 1992). This kind of generality is limited in the sense that (1) it is mechanism-free and determination of "generality" requires endless iteration of experimental permutations and (2) special cases must be explained in post hoc, case-by-case investigation. Furthermore, this view of generality provides only a limited ability to predict the outcome of novel manipulations. We believe these limitations can be avoided by focus on mechanism in experiments and by development of mechanistic theory that can explain a broader range of special cases.

As a demonstration of our position we pose the question, What is the domain of generality of patterns observed in protist food web dynamics? The answer to this question lies in the understanding of mechanisms that govern system stability and the extent to which this understanding is provided by the experimental manipulation. The patterns in time course of abundance and variance in abundance observed by Lawler and Morin were likely governed by many mechanisms; hence their experiments were mechanism-free or mechanism-vague. One uncertainty is whether abundance of food chain elements was governed by predominantly top-down or bottom-up regulation. It is likely that abundances in different treatments were affected by different mechanisms. The stability of food chains should also be affected (at a minimum) by encounter rates, prey capture success rates, and the efficiency and rate of biomass conversion of each participating element. A clear understanding of these mechanisms and their role in producing patterns of abundance in experimental communities would allow a concise statement of the degree of generality of patterns observed in these manipulations (i.e., what properties of natural systems must obtain to exhibit behavior similar to that of experimental communities). Because mechanisms are not precisely known, the domain of generality of these results cannot be exactly specified.

Hormonal Manipulations Use of hormones to manipulate phenotypes is an experimental technique that is gaining in popularity. Ketterson and Nolan (1992) and Ketterson et al. (1992) outline their rationale and provide an example of hormonal manipulation that has been referred to as "phenotypic engineering." In their own words, "Phenotypic engineering consists of manipulating the phenotype of an organism, quantifying the effects of the manipulation, and relating these effects to performance or fitness. This method permits exploration of the evolutionary significance of phenotypic variation by asking whether a rare or a novel phenotype would increase in frequency, assuming the requisite genetic variation" (Ketterson and Nolan 1992: S41). Furthermore, they suggest that "it is possible to probe the question of why existing phenotypes persist despite the fact that alternative phenotypes are possible" (Ketterson and Nolan 1992:S42).

In the context of these issues of general interest, Ketterson et al. (1992) used testosterone implants to manipulate phenotypes of male dark-eyed juncos during their reproductive season. A sample of male birds were collected while their mates were brooding the first clutch of the season. Half of the male birds received testosterone implants, and the other half received sham implants. Ketterson et al. (1992) made a series of measurements on behavior of both sexes (feeding trips to the nest, time spent brooding by females, and time spent singing by males) and related these behavioral measures to short-term fitness components (eggs laid and hatched in the first and second clutch, number of nestlings at day 10, female mass at day 10, and renesting interval). Testosterone-implanted males exhibited 200% larger home ranges than controls and 300% larger core areas, spent significantly less time at the nest and feeding young than controls, ranged greater maximum distances from the nest than controls, and sang more frequently than controls (Chandler et al. 1994, Ketterson et al. 1992). Clearly, the manipulation produced novel phenotypes whose behavior was far outside the norm for male dark-eyed juncos. Despite this massive behavioral perturbation, effects on short-term fitness components were largely undetectable. Lack of clear fitness effects was likely due to a combination of low statistical power for some measures, compensation by unmanipulated females, and the short duration of the experiments. The authors offer four possible interpretations of the observed results: (1) a wide range of equally fit phenotypes can exist, (2) fitness effects of elevated testosterone were too small to detect, (3) fitness effects were absent in this study but may be detectable at other times or in other environments, and (4) the components of fitness measured were insensitive to the manipulation, but other fitness components may be affected.

In this series of hormone manipulations, the mechanism that governs behavioral changes in male juncos is explicit. There can be little doubt that the increase in testosterone at the particular stage of male life history was directly responsible for shifts in male behavior. For this reason, we consider these manipulations to be mechanism-explicit experiments. The explicitness of mechanism allows a very clear statement of the appropriate scale and domain of generality over which the results of this experiment apply. The appropriate spatial scale for this particular mechanism is on the order of individual males—the mechanism of testosterone increase operates directly on individual patterns of behavior. The appropriate temporal scale for this particular mechanism may be defined most easily by the life history stage during which the manipulation takes place—in adult reproducing males during brooding by females of the first clutch of the year. Therefore, the domain of generality of the results of these experiments (i.e., the set of conditions under which the results of these manipulations have relevance to the stated goal of determining whether a novel phenotype would increase in frequency) includes all possible mutations that produce increases in testosterone similar in magnitude to experimental increases, produce testosterone increases in adult male dark-eyed juncos during brooding of the first clutch of the year by females, and, furthermore, produce no other discernible effects on the phenotype.

Allometric Engineering In a series of experiments, Sinervo and coworkers have manipulated trade-offs between clutch size and egg size in lizards by applying a variety of techniques, including yolkectomy and hormonal treatments at different stages of the reproductive cycle (Sinervo 1990, 1993; Sinervo and Huey 1990; Sinervo and Licht 1991). Female lizards (*Uta stansburiana*) with large clutches of small eggs were produced by increasing circulating levels of follicle-stimulating hormone (FSH) in vitellogenic females (Sinervo and Licht 1991). Yolkectomy of eggs following oviposition has been used to affect hatchling size (Sinervo 1990, Sinervo and Huey 1990). Radical yolkectomy of oviducal eggs has been used to reduce clutch size in the oviduct and thereby produce smaller clutches of larger eggs (Sinervo and Licht 1991).

The primary purpose of these elegant manipulations has been to investigate the mechanistic basis and fitness consequences of naturally occurring negative covariation between clutch size and egg or hatchling size among populations of *U. stansburiana*. These goals are made clear by the following quotes:

> The experimental manipulations of clutch and egg size address the causal basis of the physiologically based trade-off between clutch size and egg size. (Sinervo 1993: 215)
>
> Our experimental data indicate that these comparative patterns of covariation between clutch size and egg size are governed by the mechanistic bases underlying the regulation of these traits. This experimental confirmation of the comparative patterns has important implications for the adaptive evolution of clutch size and egg size. (Sinervo and Licht 1991: 260)
>
> Given the pervasive nature of the egg size and egg number tradeoff among amniotes . . . it is likely that our results might be generalizable to other groups of vertebrates. (Sinervo and Licht 1991:262)

Such statements may be found throughout the allometric engineering literature, and they imply that Sinervo and coworkers argue that they have directly manipulated the mechanistic basis whereby individual females make clutch size–egg size allocation decisions.

Through allometric engineering, Sinervo and coworkers have succeeded in mimicking the pattern of variation in clutch size–egg size trade-offs observed in among-population comparisons of *U. stansburiana*. Producing variation in the lab that is parallel to variation observed in the field, however, does not imply that the mechanistic basis of variation in the field has been discovered. A cogent statement of the domain of generality of the results of size manipulations requires consideration of the exact mechanisms being manipulated. In fact, each technique employed in this family of experiments arguably represents a different mechanism. Hatchling size manipulation through yolkectomy of recently oviposited eggs is a manipulation that may have little bearing on the actual physiological mechanisms responsible for clutch size–egg size relationships. Fundamental to the interpretation of the results of yolkectomy experiments is the assumption that size-manipulated eggs and hatchlings are equivalent in all meaningful ways with eggs and hatchlings of comparable size produced naturally. This equivalence has yet to be demonstrated (Bernardo 1991). Likewise, reduction of clutch size by radical yolkectomy in the oviduct is a manipulation applied after the female makes the primary clutch size decision. Such a manipulation may only be relevant to the actual mechanisms that establish the clutch size–egg size trade-off if it can be shown that females routinely reduce clutch size through the selective removal of yolk from a subset of available developing follicles. Of all the manipulations employed, increasing circulating FSH alone may be related to the actual mechanisms whereby female lizards make clutch size–egg size allocation decisions. The role of variation in circulating FSH in determining clutch size–egg size relationships in natural populations apparently has yet to be demonstrated and is complicated by the fact that, as yet, no radioimmunoassay for squamate FSH or its analogue is available (Sinervo and Licht 1991). We argue that these procedures do not directly manipulate the actual mechanistic basis of clutch size–egg size trade-offs, but rather, they affect phenotypes after the female has made this critical allocation decision. Even the FSH manipulation is ambiguous with respect to its relationship to actual mechanisms governing clutch size–egg size trade-offs in nature. For these reasons, with respect to the often stated goal of understanding the physiological basis of clutch size–egg size trade-offs, we consider these manipulations to be mechanism-ambiguous.

Despite the apparent mismatch between manipulations employed and the actual mechanisms that govern clutch size–egg size relationships, these experiments produce their results through explicit mechanisms. Thus, we can state explicitly that the domain of generality of the results of these experiments includes all lizard species that affect clutch size through mechanisms that are directly analogous to egg yolkectomy, radical yolkectomy in the oviduct, and variation in levels of circulating FSH.

Summary

For ecology to advance as a science, we must continually evaluate our current understanding of natural processes and the methods by which we arrive at that understanding. The uniqueness of individuals and the potential for multiple causality in patterns of importance to ecologists force a particular structure on ecological theory and experiments. In our opinion, it is the application of simplistic modeling and experimental approaches that has, in part, led to the conception of ''general'' ecological theory that explains few or no special cases. Ecological theory and experiments are of two basic types: process-explicit (mechanism-based) theory and experiments and phenomenological (mechanism-vague or mechanism-free) theory and experiments. Both types of theory and experiments are useful, but the defensible interpretations that can be drawn from each are fundamentally different. A concept of mechanism is central to the distinction between these two classes of manipulation. We have defined mechanism as a level of reductionism that provides a causal explanation of the functional relationships among a set of variables. Each mechanism operates over a particular set of spatial, temporal, and organismal scales and therefore determines these appropriate scales for experiments designed to test alternative hypotheses of causality in ecological systems. These scales, in turn, determine the domain of generality over which any causal explanation applies or over which the results of any experiment apply. That is, most ecological processes or principles are valid over a restricted range of spatial, temporal, or organismal scales (= the domain of generality of a given process or principle). For ecologists, nature is truly a collection of special cases.

Ecologists frequently overgeneralize the results of observational, theoretical, and experimental studies because of a failure to appreciate the connection between mechanism, scale, and generality. Phenomenological or mechanism-vague experiments are not explicit with regard to mechanism or scale, and therefore the domain of generality associated with these experiments is either ambiguous or zero (results apply only to the experimental system). All ecological experiments are conducted on some set of temporal, spatial, and organismal scales. However, scales of experimentation often do not match the temporal, spatial, and organismal scales over which the processes studied purport to operate. The domain of generality of experimental results cannot be explicitly stated if the experiment was mechanism-free or if the experimental scales and those dictated by the mechanism in question were mismatched. These considerations suggest that discussions of generality should be limited to situations where the set of operating mechanism (M^*) has been unambiguously identified. Clearly, it will take more than experiments alone for ecology to advance as a science. Natural history, phenomenological experiments, and process-explicit experiments all are required to increase our understanding of the natural world. We suggest only that believable statements about generality require knowledge of the relevant mechanisms. A useful practice, and one which we support, might be specifying the domain of generality of theoretical and empirical work in much the same way as we specify the methods we use to acquire data or to construct models as part of the normal reporting process. In addition, application of our definitions may clarify those instances where the domain of generality remains unknown.

Perhaps some of the problems encountered in determining domain of generality in ecology are created by limitations in our current epistemology. Unambiguously identifying the set of mechanisms responsible for a given pattern is problematic. Whereas we have clear criteria for rejecting hypotheses, when do we generally accept that a given mechanism is the correct one? Clearly, among researchers there is wide variance in willingness to attribute ecological patterns to specific mechanisms. This dilemma is at the core of the generality debate. If specification of generality requires knowledge of mechanism and if our criteria for attributing a given pattern in nature to a mechanism or set of mechanisms are to some degree subjective, what then is the prospect for generality in ecology? It is ironic that specifying the generality of a principle may require a degree of specificity that we are epistomologically ill-equipped to obtain.

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