CONTRIBUTIONS

Commentary

(Editor's Note: because of the stimulating conceptual questions it raises concerning our "common knowledge," the following discussion is being published as an exception to the Bulletin policy declining contributions that are too technical or specialized to be published without scientific review.)

On the Origins of the Lotka-Volterra Equations

Although the Lotka-Volterra equations were derived quite independently by Lotka and Volterra, they share an identical mathematical structure. However, the assumptions underlying the two respective derivations are importantly different, with the consequence that important differences in the interpretation of the parameters exist between the two formulations. Here we make these differences fully explicit to further disseminate the nontrivial implications for the application, interpretation, and scope of legitimate criticism of these equations, which may not be widely appreciated by practicing ecologists.

Generalized Lotka-Volterra (GLV) equations have a long history of use as ecological models. They are commonly used to investigate the qualitative nature of ecological dynamics, whether they be point equilibria, periodic, or chaotic behavior, and are routinely used to study the sensitivity of equilibrium stability to various parameter modifications, on which may be placed some form of ecological interpretation. Application of these structural sensitivity analyses to GLV equations has proved to be a rich seam of hypothesis generation in theoretical ecology since the introduction of these equations by Lotka (1925) and Volterra (1926). However, as pointed out by Real and Levin (1991), Lotka and Volterra formulated their equations using two fundamentally different sets of assumptions. These different formulations are only very occasionally recognized (e.g., Pimm 1982: 15), yet have important consequences for the application and interpretation of ecological models using these equations.

Lotka's (1925) formulation of the Lotka-Volterra equations implicitly recognizes the improbability (and for many applications the nonnecessity) of completely specifying the full functional forms of the equations governing an ecological system. Instead, it is assumed that within a local neighborhood of an equilibrium point, the full equations are well approximated by the first-order terms of a Taylor series. Let the per capita growth rate of species i (N_i) be represented by the unspecified function:

$$\frac{1}{N_i}\frac{dN_i}{dt} = F_i(N_1, N_2, \ldots, N_n). \tag{1}$$

The right-hand side is expanded (as a Taylor series) in the vicinity of a nontrivial equilibrium point (N_i^* 0, for all i). If terms of second and higher orders are ignored, the following linearized equations are obtained:

$$F_i(N_1, N_2, \ldots, N_n) = F_i(N_1^*, N_2^*, \ldots, N_n^*) + \sum_{j=1}^{n} \left.\frac{\partial F_i}{\partial N_j}\right|_{N_j = N_j^*} (N_j - N_j^*). \tag{2}$$

Expanding (2), writing

$$b_i = -\sum_{j=1}^{n} \left.\frac{\partial F_i}{\partial N_j}\right|_{N_j = N_j^*} N_j^* \quad \text{and}$$

$$a_{ij} = \left.\frac{\partial F_i}{\partial N_j}\right|_{N_j = N_j^*} \tag{3}$$

and noting that at a nontrivial equilibrium point $F_i(N_1^*, N_2^*, \ldots N_n^*)$, must equal zero, we see that the dynamics of the model around the equilibrium point may be approximated by the familiar GLV equations:

$$\frac{dN_i}{dt} = N_i(b_i + \sum_{j=1}^{n} a_{ij} N_j). \tag{4}$$

Derivatives defining the coefficients (Eq. 3) are evaluated at the equilibrium and will likely be defined in terms of the equilibrium population sizes.

This derivation, which we refer to as the local formulation, has considerable appeal, as it possesses great generality. Assuming that the populations stay in the neighborhood of the equilibrium point around which the full equations were expanded, this formulation is immune to criticisms that the equations are "unrealistic"; any system of equations, no matter how complex or how poorly defined, may be locally approximated by a model of the form of Eq. 4. This umbrella of generality has provided much needed shelter to theoretical ecology over the years (see for example MacArthur 1970, May 1974). However, the local nature of the formulation leads to a number of drawbacks, most importantly that questions concerning the behavior of the system far from the equilibrium point cannot be addressed. The parameters and functions are only defined "close to" and in terms of the equilibrium; there is no easy way of determining precisely what "close" really means. The position (and indeed the existence) of the equilibrium point must be assumed if the full equations are unknown; it cannot be deduced from the parameters that appear in the GLV equations. Furthermore, because the parameters (the a_{ij}'s and b_i's) are functions of derivatives evaluated at a particular equilibrium, they are not system-wide (global) constants; they will take on different values when the full equations (Eq. 1) are expanded around some other equilibrium.

Volterra's (1926) derivation was more direct; he assumed that Eqs. 4 *are* the fully specified equations governing the global dynamics of the system. Definite ecological interpretations can then be placed upon the coefficients appearing in Eq. 4; b_i is the per capita rate of change in the absence of all other species (b_i often assumed to be positive for autotrophs and negative for heterotrophs), a_{ij} describes the per capita effect of species i on species j (for example, negative if j is a predator of i, positive if i is a predator of j), a_{ii} terms may be defined as negative or zero. The nontrivial internal equilibrium point is found by setting Eq. 4 equal to zero. It is given by the product of the vector **b** (whose ith element is b_i) and the inverse of the interaction matrix **A** (whose ijth element is a_{ij}), assuming that **A** is invertible

$$\mathbf{N}^* = -\mathbf{A}^{-1}\,\mathbf{b}. \qquad (5)$$

This equilibrium may or may not be feasible ($N_i^* > 0$ for all i). Boundary equilibria may be calculated by setting some N_i^* equal to zero and solving a reduced form of Eq. 5.

This method of formulation, which we will call the global formulation, has nontrivial implications for the use and interpretation of these equations. The global formulation has several advantages. The parameters in the equations are globally defined constants having definite ecological interpretations. With one set of parameters the behavior of the system in all regions of state space can be studied. Periodic and chaotic behavior can be studied with relative ease. The equilibrium positions can be calculated in terms of the parameters in the equations. However, this formulation is likely to represent a gross simplification of the biological reality; it rests on the assertion that these equations governing the population dynamics are globally pervasive. The simplicity of the functional forms of these globally formulated equations may be legitimately questioned.

These different derivations should be of more than pedagogical or historic interest. Two important points arise from recognizing these different formulations. The first is that since only the local formulation is representative of a broader class of models, only conclusions from this formulation may lay claim to any greater underlying generality. The second is that different interpretations are placed on the parameters within the two formulations. We cannot have our cake and eat it too, claiming the generality of the local formulation while using the clear interpretation of parameters provided by the global formulation. Popular recognition of these alternate formulations would, on occasions, save theoreticians from the charge of fanciful modelling, and empiricists from measuring the wrong parameters.

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Ecological Sustainability is Fundamental to Managing the National Forests and Grasslands

The four ecologists who are members of the 13-person Committee of Scientists of the National Forest Management Act *discuss the pivotal role of ecological sciences in developing the committee's recommendations.*

The nearly 80 million hectares of national forests and grasslands in the United States are a treasure. This vast estate is a legacy of visionary conservation leaders and 100 years of dedicated efforts by USDA Forest Service stewards. Given the diverse values and expectations of the American people, it is not surprising that management of the national forests and grasslands has been controversial from the beginning. In response to heated controversy surrounding management direction, in 1976 Congress passed the National Forest Management Act (NFMA). This act assumed that conflict resolution required the development of integrated land- and resource-management plans for each national forest. Reinforcing the National Environmental Policy Act (NEPA), NFMA called for public participation in the creation of those plans. The act also mandated the creation of a Committee of Scientists to provide advice to the Secretary of Agriculture and to the Chief of the Forest Service on how best to implement the act's broad mandate.

The first Committee of Scientists met under the leadership of Art Cooper, past president of the Ecological Society of America. The 1982 regulations resulting from that committee's efforts called for provision of adequate habitat to maintain viable populations of existing native vertebrate species as well as desired nonnative vertebrate species; protection of soils, streams and watersheds; and many other conservation measures. These requirements were intended to provide a policy framework for sustaining ecological systems within which decisions could be made.

As the national forests and grasslands began a second round of NFMA land- and resource-management plans, a number of phenomena occurred that were not foreseen either by Congress when it passed NFMA or by the first Committee of Scientists when it helped develop regulations to implement the act. Ecosystem management, with its emphasis on broad landscapes that often span political boundaries, is the paradigm for stewardship. Protection and restoration of fish and wildlife populations are critical under both the Endangered Species Act and NFMA. The public is now interested in sharing stewardship responsibilities for the national forests and grasslands. Increasingly, federal, state, and local agencies collide as they implement various statutes related to the protection and use of the environment. The Forest Service and Congress continue to budget monies by specific programs, thus undermining the ability of forests to implement balanced plans. Deep divisions remain over the management of the national forests and grasslands.

In December 1997, Secretary of Agriculture Dan Glickman convened a second Committee of Scientists to review and evaluate the Forest Service's planning process for land and resource management and to identify changes that might be needed in the planning regulations. This interdisciplinary committee met in cities around the country, where it heard from Forest Service employees, representatives of tribes, state and local governments, related federal natural-resource agencies, and members of the public.

The committee includes four ESA members from landscape ecology, fire ecology, silviculture, and wildlife biology, as well as representatives of economics, sociology, collaborative planning, environmental law, range management, and fisheries. Their report concludes that ecological sustainability is the fundamental basis for economic and social sustainability. This finding does not mean that the Forest Service should maximize the protection of plant and animal species or provide environmental protection to the exclusion of other human values and uses. Rather, it means that planning for the multiple use and sustained yield of the resources of national forests and grasslands should ensure the sustainability of ecological systems and native species. Without ecologically sustainable systems, other uses of the land and its resources may be impaired.

Ecological sustainability: a necessary foundation for stewardship

Setting ecological sustainability as a key goal acknowledges that ecological systems provide many outputs that humans require. That is, human health and the integrity of ecological systems are inseparable objectives. While the scientific community can help estimate the impacts associated with management strategies, decisions about an acceptable level of effects are value-based, not science-based, decisions. Furthermore, the human values, needs, uses, and ecological condition of each locality will change with time. Policy and management must evolve according to natural dynamics and disturbances as well as social events, economic change, and political values. Nonetheless, it is clear that ecological sustainability provides a necessary foundation for national forests and grasslands to contribute to economic and social well-being—supporting dynamic economies and creating opportunities for enduring human communities. Therefore, planning must acknowledge the following features of ecological systems:

- The significance of natural processes
- The dynamic nature of ecological systems
- The uncertainty and inherent variability of ecological systems
- The importance of cumulative effects.

These features of ecological systems led to the need to preserve options in developing management plans. Preserving options presumes that a range of acceptable choices will be available to address the environmental problems confronting people in future generations. Preserving options is also a way of explicitly acknowledging our incomplete understanding of complex ecological systems. Therefore, this philosophy is an expedient touchstone for managing the national forests and grasslands.

The concept of ecological sustainability requires that national-forest planning and management consider the context of the landscape, which often includes lands and communities beyond the boundaries of the national forests and grasslands. National forests and grasslands are open systems that are affected by the land uses outside their boundaries. Thus, the characteristics of the land, the ways that people interact with it, and what they expect from it must be assessed in terms of ecological sustainability.

The committee concluded that conserving habitat for native species and the productivity of ecological systems remains the surest path to maintaining ecological sustainability. The committee suggests using two approaches in tandem to conserve these key elements of sustainability. First, a scientific assessment of the characteristic composition, structure, and processes of the ecosystems is needed. This assessment should provide an understanding of the "ecological integrity" of the planning area. Ecosystems with integrity maintain their characteristic species diversity and ecological processes, such as productivity, soil fertility, and rates of biogeochemical cycling. Because ecosystems are dynamic and variable, the concept of the "historic range of variability" is used to characterize the variation and distribution of ecological conditions occurring in the past. This concept allows us to compare the ecological conditions that will be created under proposed management scenarios with past conditions. The more that prospective conditions differ from conditions during recent millennia, the greater the expected risk to native species, their habitats, and their long-term ecological productivity.

Second, the concentration should be on the viability of native species themselves. Because monitoring the status of all species and assessing their viability is impossible from a practical standpoint, it is necessary to pay most attention to a subset of species called "focal species." The key characteristic of focal species is that collectively their abundance, distribution, health, and activity over time and space indicate the functioning of the ecological system. Through monitoring, the habitat needs of the focal species can be analyzed, and projections can be made to determine the type and amount of habitat needed for the species to have self-sustaining populations well distributed throughout its range. Self-sustaining populations, in turn, are those that have sufficient abundance and diversity to display the array of life history strategies and forms that provide for their persistence and adaptability in the planning area over time. The habitat created or maintained under any management scenario may be compared with the habitat needed for the viability of each selected focal species. The less adequate the habitat for each focal species, the greater the risk to other native species and ecological productivity. Therefore, the committee suggests a three-pronged strategy: (1) concentrate on a set of selected focal species and their habitat needs, (2) maintain conditions necessary for ecological integrity, and (3) monitor the effectiveness of this approach in conserving native species and ecological productivity.

Implementing science-based stewardship

To ensure the development of a scientifically credible stewardship strategy for the national forests and grasslands, the committee recommends a process that includes (1) science-based selection of focal species for the development of measures of species viability and ecological integrity and for definition of key elements of conservation strategies; (2) independent scientific review of proposed conservation strategies before plans are published; (3) scientific involvement in designing monitoring protocols and adaptive management; and (4) a national scientific committee to advise the Chief of the Forest Service on scientific issues in assessment and planning.

Assessments are a critical component of the framework proposed by the committee; assessments provide the foundation of independent information upon which to build conservation strategies and management decisions and against which alternative approaches can be evaluated and modified. These assessments should be conducted at both the bioregional scale and a smaller scale, such as a watershed. Assessments over large areas ("bioregions"), such as the Sierra Nevada or the Northern Spotted Owl region, will generally be needed to provide the context for landscape-level strategic planning. Assessments at the more local level, such as watersheds, are needed to translate strategic plans for large landscapes into site-specific management actions. In some cases where the bioregional assessment is at a very large scale (e.g., the Columbia River Basin assessment), an intermediate scale of analysis may be needed. Nearly half of the National Forest System lands have had a recent bioregional assessment of some form.

Decisions should occur at the scale of the issue or problem. For example, policies regarding conservation strategies for wide-ranging species need to be developed at the bioregional level to encompass the entire range of the species. Similarly, strategic planning is generally needed at a large-landscape level that follows ecological and political or social boundaries. Naturally, implementation planning occurs at a small-landscape level where actions, cumulative effects, and performance can be monitored.

Collaborative planning would provide a means of reaching agreement about a common vision regarding the future conditions of the national forests and grasslands and regarding their unique contributions to different regions of the country. Because of this commitment to a common vision and a shared goal of sustainability, collaborative planning efforts bring people together at different geographic scales, across political and administrative boundaries, and from different parts of society to craft strategies and actions that make a difference and have worthwhile results. The key elements of collaborative planning are:

- making “desired future conditions” and the outcomes associated with them the central reference points for planning;
- establishing pathways to the desired future conditions and outcomes, and orienting performance measures, monitoring, and budgeting to making progress along those pathways;
- supporting local-management flexibility with independent field review;
- keeping decisions close to the planning area;
- emphasizing ecological boundaries for assessment and planning but also considering their social meaning;
- addressing all federal lands within the area, and working, so far as is feasible, with all affected federal agencies;
- moving toward integrated administration of jurisdictionally fragmented areas;
- using the NEPA review process as an opportunity to coordinate across agencies and jurisdictional responsibilities;
- using principles of efficiency analysis in planning and management; and
- identifying the suitability of land for resource management as an outcome of planning.

From the first congressional guidance on management of the forest reserves in 1897 to the NFMA in 1976, watersheds and timber supplies have been singled out for special legislative attention. Because watershed and timber issues are, by statute, central management purposes of the Forest Service, the committee made six recommendations regarding them.

1) Develop a strategy for conserving and restoring watersheds.

2) Recognize the role of timber harvest in achieving sustainability.

3) Develop flexible restocking requirements that allow for natural regeneration.

4) Select the silvicultural system, regeneration harvest method, and size of timber harvest areas to promote sustainability.

5) Recognize the need for predictable timber supplies and how adherence to sustainability increases predictability.

6) Focus planning, budgeting, and monitoring on desired conditions and the actions needed to produce these conditions.

Under the committee’s recommendations, forest management actions in the future would be guided by a comparison of the existing condition with the desired future condition. Where timber harvest is scheduled, management actions should be stated as a prescription that focuses on the actions needed to achieve or maintain the desired ecological processes, structure, and composition.

Conclusion

The implications of ecology for land management are a critical part of the report of the Committee of Scientists. The report calls for a tighter link between research and land management. It also provides an example of the impact that new developments in ecology have on applications of the science. In this case, land management has greatly benefitted from the development of new tools (e.g., geographic information systems, new modeling approaches, and new ways to integrate and analyze information). In the past 20 years, land management has been affected by the development of new fields of ecology (e.g., landscape ecology, conservation biology, and ecological economics), new theories (e.g., hierarchy theory), and new areas of application (e.g., global change). Thus, the Committee of Scientists report illustrates how science applications influence research and how research can drive applications.

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Identify Tardy Reviewers?

Without delving into the shortcomings of anonymous peer review, I would like to propose one small change that could speed turnaround by manuscript reviewers. Everyone, it seems, has had one or more publications significantly delayed because reviewers have failed to return their comments to the editor in a timely fashion. Although we all are busy, if we agree to undertake a review it should be done promptly. However, anonymous reviewers have little to lose by being slow on a review. No one beyond the journal's editorial staff knows who the slackers are.

In the issue where editors acknowledge reviewers for the year, I would suggest the editors also include the mean response time for those reviewers. I do not believe this would encompass much additional work for the managing editor. Reviewers who consistently return reviews promptly will be evident, as will those who consistently procrastinate. Knowing that such a statistic will be published might motivate some reviewers to get on with it more promptly. Likewise, others who realize they don't "really" have the time to review a manuscript might be more inclined to decline the editor's request for a review.

The reviewers for ESA are, perhaps, less guilty of sluggish response time than some other journals. Thus, the ESA could be a leader in implementing such a policy. If other journals follow the lead, we all might benefit.

Cheers,

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Reply

This is an interesting idea, but we suspect that the threat of posting mean response times with our acknowledgment of reviewers would not help speed up the review process. In fact, it could make the problem worse if some individuals became reluctant to review for our journals. There is also a small but significant risk that the policy Mack proposes could compromise reviewer anonymity.

We certainly do not want to risk alienating members of our reviewer pool. The high quality of our publications depends in large part on their volunteer efforts.

We appreciate the suggestion, however, and we welcome further ideas about how we might attack the perennial problem of tardy reviewers.

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