

Biological Diversity, Ecological Integrity, and Neotropical Migrants: New Perspectives for Wildlife Management

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Abstract — New initiatives in wildlife management have come from the realization that birds can be used as indicators of ecosystem health. Conceptually, biological diversity includes processes working at all scales in biological hierarchies that compose the natural world. Recent advances in the understanding of ecological systems suggest they are nonequilibrium systems, and must be managed as such. In a practical sense, biological diversity must be managed by devising indicators of ecosystem integrity and health. Ecological integrity, although there are difficulties in defining criteria for its measurement, provides a conceptual focus for management decisions that are intended to preserve biodiversity. More importantly, tools for devising objective measures of the ecological integrity of a community are readily available. Management of bird communities can be based on indices of ecological integrity that incorporate presence and relative abundances of neotropical migrants. Neotropical migratory birds provide an ideal focus for such management tools, since they have been shown to be highly sensitive to changes in landscapes that compromise the spatial continuity and integrity of natural ecosystems. In order to accommodate new concerns for preservation of biodiversity, wildlife managers must acquaint themselves with new tools and approaches. In particular, an expanded geographic scale perspective should permeate management activities.

INTRODUCTION

Birds have always been viewed as important indicators of ecosystem health. They are top predators, have relatively low birth rates and long lifetimes, and therefore have populations that seem to be extremely sensitive to environmental variability. Indeed, the origin of widespread concern in society today regarding environmental issues can be traced back to Rachel Carson's *Silent Spring*. Both economic development and management of natural resources have been greatly affected by this concern. Government agencies have been mandated by law to manage natural resources in a way that maximizes not only for consumption, but for uses consistent with preservation of the ecosystems containing those resources.

In this paper, I consider how management activities aimed at preserving neotropical migrants can be used as templates for preservation of the ecological integrity (Karr 1991) of ecosystems in which they reside. I will consider only one aspect of system integrity, namely, biological diversity. My approach is to ask the question "How can the diversity of neotropical migrants serve as an indicator of the ecological integrity of ecosystems?" I hope to provide an overview of how management decisions aimed at preserving habitat for neotropical migrants can have as an added benefit, the preservation of entire ecosystems and their attendant ecosystem services. I believe management for neotropical migrant biological diversity can be consistent with sustainable use of natural resources for consumption and economic development. The key word here is "sustainable", because it is abundantly clear from past experience that unsustainable uses of natural resources ultimately lead to ecosystem degradation.

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First, I will consider the problem of defining biological diversity. Clearly, it is important to define biological diversity in such a way that it can be used in developing and implementing management decisions. Next, I consider the problem of the integrity of ecosystems and how it can be evaluated. Finally, I discuss how specific management decisions affecting neotropical migrant habitat can be used to enhance ecological integrity of the ecosystems in which they reside.

CHANGING ECOLOGICAL PARADIGMS

Most ecological textbooks define species diversity as the number of species found in a given area (e.g., Ehrlich and Roughgarden, 1987; Begon, Harper, and Townsend, 1990; Ricklefs, 1990; Smith, 1990). This has traditionally been the basis for discussions of biological diversity. Although it is an empirically tractable exercise to count the number of species in a given area, such a procedure ignores many potentially important phenomena. A broader definition of biodiversity includes both the number of species and extent of their genetic variability (see, e.g., Office of Technology Assessment [OTA], 1987). The OTA definition explicitly includes systems of different sizes, ranging from biochemical variation in DNA to number of species in ecosystems (see also Norse et al. 1986). Hence, in its broadest definition, biological diversity is the manifestation of virtually every biological process known.

Biodiversity: A Complex Issue

In discussing biological diversity, it is important to realize that ecological systems are highly complex, and therefore, any management policies or decisions dealing with biodiversity are themselves going to be complex. A number of recent authors have focussed on the problem of how to understand the workings of complex biological systems (Allen and Starr 1982, Eldredge 1985, Salthe 1985, O'Neill et al. 1986). The common thread among these approaches is that biological systems have a hierarchical structure. Unfortunately, there are several relevant ways to construct a hierarchical ordering scheme that might be applicable to the problem of biological diversity. Biological systems participate in a number of different sets of processes. Three of the most meaningful from the perspective of biological diversity are genetical processes, ecological processes, and phylogenetic processes. Genetical processes are concerned with storage, maintenance, and transmission of information regarding biological structure. Phylogenetic processes are closely related to genetic phenomena, but emphasize and elaborate patterns of similarity of descent among species and higher taxa. Ecological phenomena involve exchanges of matter and energy among biological units and their environments.

Each of these processes affect biological diversity and should influence policies dealing with its management. Genetic processes determine the amount and kinds of variation that exist

in a species that might be important to its ability to maintain viable populations. Phylogenetic information is critical in conservation because in order to assess species losses, we first have to be able to count them. Ecological processes, the traditional focus of management agencies, determine the proximate mechanisms by which populations persist, and provide many of the tools for the active management of biodiversity.

Changing Paradigms in Ecology: Attempts to Deal with Complexity

Wildlife management developed in an era when ecologists emphasized the stable nature of ecosystems and communities. The predominant models of population dynamics emphasized that populations had equilibria towards which they grew (or declined). The idea of carrying capacity is a direct translation of this idea. Habitats were thought to have limits on the abundance of each species determined by the amount of resources, competitors, and predators. Succession was thought to proceed to well defined endpoints, the so-called climax communities of Clements and others.

Because of the empirical difficulties inherent in this equilibrium view of nature, ecologists now seem to be moving away from it in favor of a new paradigm (Botkin 1990, Pickett et al. 1992). I believe that this has important implications for the way we should go about conserving biological diversity. I will attempt to characterize this new paradigm, then, in the next section will deal with how we might approach assessments of habitats in the face of these new ideas emerging in ecology.

There are three characteristics that I see as common themes in the "nonequilibrium" paradigm in ecology. The first is that emphasis is placed on dynamics rather than equilibria. Ecologists are much more interested in how communities and ecosystems change rather than attempting to explain the nature of endpoints of that change. In fact, many ecologists don't think that there are any stable endpoints towards which populations, communities, or ecosystems converge. The second idea emerging in this new approach to ecology is the hierarchical nature of populations (Morris 1987), communities (Maurer 1985, 1987; Kolasa 1989), and ecosystems (Allen and Starr 1982, O'Neill et al. 1986). This means that scale of observation and the context in which a system operates are critical components of a complete understanding of any population, community, or ecosystem process. In this view, "top down" constraints on the behavior of the system are as important as "bottom up" processes. That is, to understand the changes in population abundance of a species in a particular habitat, we need to know not only what resources and biotic interactions within the habitat affect vital rates of the population, but we need to know the geographic context (is the population near the periphery of its range?), the phylogenetic context (how has the evolutionary history of the species affected its ecological attributes?), and the landscape context (how are the rates of immigration and

emigration affected by the structure of the landscape?). Finally, because of this emphasis on hierarchical structure and context sensitive processes, most ecologists explicitly emphasize the spatial context of ecological processes. For example, an enhanced understanding of the conservation of populations is emerging from studies which explicitly include the spatial structure of populations in changing landscapes (Lamberson et al. 1992, Pulliam et al. 1992).

ECOLOGICAL INTEGRITY

Current views regarding ecological systems, then, emphasize the diverse and complex nature of interactions among organisms and between organisms and their environment. This view, however, has not been integrated with wildlife management. In this section, I consider the problems of defining properties of ecosystems that can be useful in assessment of ecological change in the face of complexity.

The Ecological Context

As indicated above, traditional views of biological diversity have focussed on the idea that ecosystems will return to a predetermined stable state after a perturbation. Ecosystems are often depicted as "entities" which remain relatively unchanged if left alone. The traditional metaphor used in this context has been "the balance of nature" (Pickett et al. 1992). The balance of nature metaphor has had a powerful impact on management for biological diversity. For example, a significant amount of management by the Park Service as been centered around a "let it alone" philosophy. In many instances, human activities in ecosystems are viewed as alien influences, and sometimes value judgements are attached to them by calling them "destructive". Even the concept of a "natural" ecosystem is influenced by the equilibrium paradigm of ecology. Any system influenced by people cannot be considered "natural". The solution to management problems under such a scheme is to attempt to *remove all human influences, then let the ecosystem "heal itself"* through natural processes of ecological change. Oftentimes such management approaches neglect traditional habitat management practices which are deemed "artificial". This "hands off" approach is often integrated into endangered species management, even when traditional wildlife management techniques might be fruitfully applied.

This mindset on equilibrium, especially when it relates to the preservation of biological diversity, has continued despite failure of the equilibrium paradigm to provide a meaningful theoretical basis for ecosystems (Pickett et al. 1992). For example, the equilibrium models of community structure of MacArthur (1972) and his colleagues have been roundly criticized for not being adequate to explain most of what goes on in ecosystems (see, e.g., Wiens 1983, 1984, 1989 for examples pertaining to birds). Communities have been found

not to converge on single equilibria, but instead to change towards multiple states by a variety of pathways (see references in Pickett et al. 1992).

Pickett et al. (1992) suggest that a better metaphor to describe natural systems might be "the flux of nature". Mounting evidence suggests ecosystems are not static, unchanging entities that can be left alone to heal themselves. Management activities to enhance biological diversity must take into account the dynamical nature of ecosystems (Landres 1992). This means that management decisions must have information from more than just the local area being managed. Managers should be aware of the functional nature of components of the ecosystems they must manage. Management decisions cannot end at convenient political boundaries, but must incorporate effects of processes occurring outside boundaries defining the unit being managed.

The ecological context in which management decisions must be made have important implications for how ecological integrity is defined. It is not enough to ask what the "natural" or "unaltered" state of the system to be managed is. Ecological integrity must incorporate the dynamic nature of ecosystems into its framework. In the next section I consider definitions of ecological integrity and how it might be measured, with special reference to birds.

Measuring Ecological Integrity: the Role of Data on Biodiversity

A widely recognized definition of ecological integrity was given by Karr and Dudley (1981), who emphasized its use in the assessment of water quality. They defined ecological integrity as the ability of an ecosystem to maintain "a balanced, integrated, adaptive community of organisms having a species composition, diversity, and functional organization comparable to that of the natural habitat of the region." Note that this definition is explicitly comparative. That is, ecological integrity is a relative attribute of an ecosystem that only has meaning when compared to another ecosystem. Clearly, Karr and Dudley intended for one of the ecosystems in the comparison be "natural." The advantages of this definition is that it is operational in the sense that quantities such as species abundances, diversity, etc., have specific meanings associated with them and metrics used to calculate them. Furthermore, Karr and Dudley (1981) argued that such quantities can be used to monitor water quality, and Karr (1991) reviewed many successful applications of the approach they outlined. This is especially appealing for land managers interested in diversity of neotropical migrant birds. It suggests that using conventional ecological statistics to measure the abundance and diversity of bird communities can provide information, even if that information is indirect, about the ecological integrity of an ecosystem.

The disadvantage of Karr and Dudley's (1981) definition is that it requires a judgement as to what defines the "natural habitat" of a region. This presupposes there is an unaffected set

of habitats that can be compared objectively with altered sets of habitats. The perspective described in the last section suggests that in reality, each individual landscape to be managed, whatever its size, is biologically and ecologically unique (Pickett et al. 1992). This uniqueness comes from the fact that each landscape has undergone numerous ecological changes over time on a number of different temporal scales. The number of such events that each community goes through is extremely large, and there is no guarantee that each community will respond in a similar fashion. Furthermore, virtually any landscape, including wilderness landscapes, bear, to varying degrees, the imprint of human activities, because ecosystem impacts can be transported into an ecosystem from sources many kilometers distant (Pickett et al. 1992). Defining the natural community in such landscapes will be very difficult.

Despite these difficulties, there are a few guidelines used to apply the concept of ecological integrity to bird communities. First, Knopf (1992) argued that communities dominated by exotics and generalist species can be considered a sign of degradation of an ecological system (see also Gray 1989). Given the myriad of processes that change a community over time, natural communities are thought to be composed of a number of specialist species that persist due to the existence of special habitat elements resulting from disturbances and other processes. Human impacted ecosystems, on the other hand, tend to be simplified so that natural processes like fire, that create specialized habitat features, are altered or suppressed. The result is "biosimplification" (Sampson 1992), that is, ecosystems that are more uniform in species composition, physical structure, and functional organization. Exotic species and generalists tend to be favored in such systems. A second guideline is that the health or performance of individual organisms tends to be better in natural systems. In aquatic systems, it is relatively easy to assess the number of individuals that show injuries, mutations, or other abnormalities (Karr 1991). For birds, this is much more difficult. However, there are methods to assess individual performance. For example, Villard et al. (1993) have shown that pairing success for male Ovenbirds in forest fragments is lower than in continuous forest so that males in fragments have a higher likelihood of remaining unpaired during the breeding season than males in continuous forests. One could also monitor nesting success, or other measures of reproductive success, to assess individual health.

Using measures of community structure and composition as indicators of ecological health or integrity of an ecosystem can provide a powerful tool for evaluating management alternatives. Community parameters of birds are sensitive to temporal and spatial changes in ecosystems. Different parameters often reflect different ecological processes (Maurer 1985). What is missing is a formalized system of sampling bird communities and deriving indices of biological integrity (Karr 1987, 1991) from those samples. Such a protocol would necessarily go beyond the Habitat Evaluation Procedures (HEP) devised by the U.S. Fish and Wildlife Service, and used widely in environmental impact assessments. It would require intensive

censuses of bird communities and detailed statistical analysis of results, both according to predetermined procedures. Success of such procedures in water quality assessment (Karr 1991) should stimulate efforts to develop a similar system for birds.

The key to carrying out an assessment of biological integrity using bird communities is the development of an index of biological integrity (IBI). To construct an IBI, a set of community characteristics are chosen, and for each, its value is ranked based on the similarity between the observed community and that expected of a "natural" community. The ranks for each characteristic are then summed, and the overall score used as an numerical estimate of how close the community is to being in a natural state. Karr (1991) lists useful characteristics for developing an IBI for a community. I used his list as a template to devise a potential list of community characteristics that might be useful for bird communities (Table 1).

Determining the "natural" state of a bird community will be difficult in many cases. The obvious approach would be to take a landscape similar to the impacted landscape being evaluated, and use it as the baseline for comparisons. This is often done in studies of forest fragmentation, where forest fragments of various sizes are compared with large, extensive forest tracts. In landscapes sufficiently altered by human activities, such opportunities may be lacking. One possible alternative is to assemble from the literature a list of those species judged to be native to the landscape of interest. It is often possible to get some idea of relative abundances from the literature. This baseline list can be used to compare to abundances obtained from intensive censuses to establish ranking criteria to calculate an IBI.

MANAGEMENT OF HABITATS FOR INTEGRITY OF BIRD COMMUNITIES

Difficulties with Applying Traditional Wildlife Management Principles

Traditional habitat management has focussed on the perpetuation of harvestable populations of game species (Leopold 1933, Peek 1986). Such efforts often leave landscapes with a high degree of "edge" habitat, because for many large game species, a number of habitat elements are required to maintain healthy populations. It has often been assumed that interspersions of habitat types created by such management is ideal for nongame species as well. If we have learned anything from studying populations of neotropical migrants it is that this is not true for many specialist species. Many neotropical migratory species of greatest concern have relatively narrow habitat requirements found only in relatively large tracts of forest (e.g., Cerulean Warbler, Robbins et al. 1992). Management practices that break up forests and create lots of edge situations are detrimental to some neotropical migrants. This was first evident from Gates and Gysel's (1978) results that showed high

Table 1. — Community characteristics and metrics that might be used in developing an index of biological integrity for bird communities which in their natural state would include a significant number of neotropical migrants.

Level of organization	Attribute and suggested metrics
Individual	Nestling growth rates, clutch sizes, & nesting success Pairing success and site fidelity Foraging behavior Parental care
Population	Density or total population size (in fragmented habitats) Incidence functions - proportion of patches occupied as a function of patch area or productivity Population variability Extinction likelihood Population age structure
Community	Species richness Relative abundances of species Number and relative abundances of neotropical migrants Number and relative abundances of habitat specialists Degree of dominance by generalist species and exotics Abundance of brood parasites and predators

rates of nest failures in artificially created edges, and has since been substantiated by a number of studies (Wilcove 1985, Askins et al. 1990, Robinson 1992).

The traditional approach to wildlife management focusses on single species. The idea is that if we create appropriate habitat elements for that species, we can maintain healthy populations for an extended period of time. In this respect, objectives of traditional habitat management are not adequate for preserving biological diversity, and some conservation biologists have been critical of traditional wildlife management activities because of this. However, the strength of the traditional approach is that it explicitly uses and enhances *natural processes* to preserve populations. In this respect, wildlife management is different from agricultural practices, which construct artificial ecosystems to perpetuate a single crop species. What is needed for preservation of biological diversity in general, and for the preservation of healthy bird communities, specifically, is a new management ethic which takes the best from traditional wildlife management and merges it with a broadened set of management objectives (e.g., Sampson and Knopf 1982). I discuss some of these new management principles in the next section.

Emerging Principles of Habitat Management for Biodiversity

Principle 1 - Diversity, per se, is not necessarily the best criteria upon which to build management objectives. Sampson and Knopf (1982) argued that many local scale management practices that encourage diversity within local communities ignore larger scale problems of maintaining viable populations of endemic or native species within a landscape. Often, high diversity in local communities may be associated with presence of many exotic species, such as European Starlings and House Sparrows, and of generalist species not specifically adapted to the native vegetation of the landscape, such as American Robins, Blue Jays, and Brown-headed Cowbirds. Many exotics and generalists not only are not adapted to native vegetation, but can be detrimental to native birds as competitors, predators, and nest parasites.

Principle 2 - The spatial structure of habitats in a landscape is important (Martin 1992). In complex landscapes, populations of different species are profoundly impacted by size, shape, and degree of isolation of habitat patches. This is particularly true

for neotropical migrants (Villard 1991, Villard et al. 1992). Wildlife managers should be trained in principles of landscape ecology. More research is needed to determine how landscape structure affects population dynamics of species, and in turn, how this influences ecological integrity.

Principle 3 - The geographical context of a management situation must influence the management approach (Sampson 1992). It is becoming increasingly clear that attention to local details in habitat management is not enough to ensure integrity of ecosystems in managed landscapes. Conservation biologists have used island biogeographic arguments to suggest policies for maintaining communities in island-like settings. However, it is becoming increasingly clear that these approaches are too simplistic (e.g., Simberloff and Cox 1987). Small islands of natural or old growth vegetation face a situation more akin to Brown's (1971, 1978) findings on mammals on mountaintops in western North America. These communities have suffered profound declines in diversity of nonvolant mammal species after being separated from one another after the climate warmed in the late Pleistocene. Likewise, reserves and other isolated patches of habitat can be expected to experience profound losses of diversity. In effect, the old connections that these habitats had with similar habitat are being replaced with new connections to the surrounding landscape matrix. Geographically, this appears to be increasing the degree to which neotropical migrant geographic ranges are becoming fragmented (Maurer and Heywood 1993). Integrity of ecological islands should be reflected in extinctions of species typical of historical vegetation of the area and in colonization of exotic and generalist species (Karr 1987, Gray 1989).

Principle 4 - Management objectives must account for natural levels of environmental variability (Landres 1992). Ecosystems should not be thought of as equilibrium systems when making management decisions. Managers should try to base management plans with change in mind. This will usually require more conservative approaches to preservation of key habitats. Since population persistence is closely tied to habitat size, larger tracts of important habitat should be preserved than would be needed under the assumption of equilibrium.

Principle 5 - Wildlife management must become a global discipline. Problems faced by virtually all wildlife extend beyond traditional political boundaries. This is particularly true for neotropical migrants, where problems cross national borders. Management objectives need to consider how management activities at one place will impact or affect other ecosystems and landscapes beyond the boundaries defined by traditional wildlife management.

CONCLUSIONS

It is clear that agencies responsible for management of habitats are facing new challenges defined in part by a better understanding of how ecosystems work, and in part by increased awareness by the public of environmental concerns. Expanding

human populations and increased rates of consumption of natural resources have created increasingly intense pressures that continue to transform natural ecological systems into human dominated ecosystems at alarming rates. In human dominated landscapes, biological diversity is much lower than in natural landscapes.

Defining what biological diversity is has been difficult since the term in its broadest meaning encompasses nearly every biological process known. Traditional wildlife and natural resource management interfaces with biological diversity through ecological integrity, that is, the degree to which a community resembles a natural, relatively undisturbed (by human activities) community. Despite the problems of defining exactly what the natural state of a community is, it is important that management decisions incorporate biological integrity of the community being managed as a prime consideration in management objectives and decisions.

In this volume, contributions will be centered around defining those specific attributes of bird communities that should define what a "healthy" bird community should look like. The presence and relative abundances of neotropical migratory species figure prominently in these definitions. These species are sensitive to a number of changes in ecosystem health, and it is likely that we will be able to develop specific protocols that can be used to evaluate the health and integrity of an ecosystem by examining IBI's constructed for bird communities.

Habitat management techniques that encourage natural processes, such as succession, fire, etc., should continue to be a part of the repertoire of land managers seeking to preserve biological diversity. But our experience with neotropical migrants has taught us that managers will need an expanded toolbox. Considerations of habitat size, shape, and connectivity must be taken into account in management decisions. In many instances, necessary management activities may include establishing networks of reserves within an intensively managed landscape that provides for the preservation of a significant proportion of the landscape in native, or "old growth", vegetation.

The implementation of such management activities requires a "top-down" approach (Sampson and Knopf 1982), that is, managers must be aware of vegetation and associated animal communities native to an entire biotic region (Sampson 1992). These associations of plants and animals have had a long history of evolutionary interactions, and such continued evolution cannot occur in small, isolated fragments of habitats. Successful preservation of biological diversity ultimately means preservation of entire ecoregions and biogeographic units across continents such that landscapes within these regions serve as sources and corridors for species native to the region. This in turn requires a sufficient amount of habitat within landscapes are capable of maintaining viable populations of native species for a long period of time. Wildlife management can no longer be carried out by isolated state and federal agencies, each tending to its own affairs.

LITERATURE CITED

- Allen, T.F.H., and T.B. Starr. 1982. *Hierarchy*. University of Chicago Press, Chicago.
- Askins, R.A., J.F. Lynch, and R. Greenberg. 1990. Population declines in migratory birds in eastern North America. *Current Ornithology* 7:1-57.
- Begon, M., J.L. Harper, and C.R. Townsend. 1990. *Ecology, individuals, populations, and communities*. Blackwell Scientific, Boston.
- Botkin, D.B. 1990. *Discordant harmonies: a new ecology for the twenty-first century*. Oxford University Press, New York.
- Brown, J.H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. *Am. Nat.* 105:467-478.
- Brown, J.H. 1978. The theory of insular biogeography and the distribution of boreal birds and mammals. *Great Basin Nat. Memoirs* 2:209-227.
- Ehrlich, P.R., and J. Roughgarden. 1987. *The science of ecology*. MacMillan, New York.
- Eldredge, N. 1985. *Unfinished synthesis*. Oxford University Press, Oxford.
- Gates, J.E., and L.W. Gysel. 1978. Avian nest dispersion and fledgling success in field forest ecotones. *Ecology* 59:871-883.
- Gray, J.S. 1989. Effects of environmental stress on species of rich assemblages. *Biological J. Linnean Society* 37:19-32.
- Karr, J.R. 1987. Biological monitoring and environmental assessment: a conceptual framework. *Environmental Management* 11:249-256.
- Karr, J.R. 1991. Biological integrity: a long-neglected aspect of water resource management. *Ecological Applications* 1:66-84.
- Karr, J.R., and D.R. Dudley. 1981. Ecological perspective on water quality goals. *Environmental Management* 5:55-68.
- Knopf, F.L. 1992. Faunal mixing, faunal integrity, and the bio-political template for diversity conservation. *Trans. North American Wildl. Nat. Res. Conf.* 57:330-342.
- Kolasa, J. 1989. Ecological systems in hierarchical perspective: breaks in community structure and other consequences. *Ecology* 70:36-47.
- Lamberson, R.H., R. McKelvey, B.R. Noon, and C. Voss. 1992. A dynamic analysis of northern spotted owl viability in a fragmented forest habitat. *Conservation Biology* 6:505-512.
- Landres, P.B. 1992. Temporal scale perspectives in managing biological diversity. *Trans. North American Wildl. Nat. Res. Conf.* 57:292-307.
- Leopold, A. 1933. *Game management*. Charles Scribner, New York.
- MacArthur, R.H. 1972. *Geographical ecology*. Harper and Row, New York.
- Martin, T.E. 1992. Landscape considerations for viable populations and biological diversity. *Trans. North American Wildl. Nat. Res. Conf.* 57:283-291.
- Maurer, B.A. 1985. Avian community dynamics in desert grasslands: observational scale and hierarchical structure. *Ecological Monographs* 55: 295-312.
- Maurer, B.A. 1987. Scaling of biological community structure: a systems approach to community complexity. *Journal of Theoretical Biology* 127:97-110.
- Maurer, B.A., and S.G. Heywood. 1993. Geographic range fragmentation and abundance in neotropical migratory birds. *Conservation Biology*, in press.
- Morris, D.W. 1987. Ecological scale and habitat use. *Ecology* 68:362-369.
- Norse, E.A., K.L. Rosenbaum, D.S. Wilcove, B.A. Wilcox, W.H. Romme, D.W. Johnston, and M.L. Stout. 1986. *Conserving biological diversity in our national forests*. The Wilderness Society.
- Office of Technology Assessment. 1987. *Technologies to maintain biological diversity*. OTA-F-330. U.S. Government Printing Office, Washington, D.C.
- O'Neill, R.V., D.L. DeAngelis, J.B. Waide, and T.F.H. Allen. 1986. *A hierarchical concept of ecosystems*. Princeton University Press, Princeton, New Jersey.
- Peek, J.M. 1986. *A review of wildlife management*. Prentice-Hall, Englewood, N.J.
- Pickett, S.T.A., V.T. Parker, and P.L. Fiedler. 1992. The new paradigm in ecology: implications for conservation above the species level. Pages 65-88 in P.L. Fiedler and S.K. Jain, eds. *Conservation biology*. Chapman and Hall, New York.
- Pulliam, H.R., J.B. Dunning, Jr., and J. Liu. 1992. Population dynamics in complex landscapes: a case study. *Ecological Applications* 2:165-177.
- Ricklefs, R.E. 1990. *Ecology*, 3rd ed. Freeman, New York.
- Robbins, C.S., J.W. Fitzpatrick, and P.B. Hamel. 1992. A warbler in trouble: *Dendroica cerulea*. Pages 549-562 in Hagan, J.M., III, and D.W. Johnston, eds. *Ecology and conservation of neotropical migrant landbirds*. Smithsonian Institution Press, Washington, D.C.
- Robinson, S.K. 1992. Population dynamics of breeding neotropical migrants in a fragmented Illinois landscape. Pages 408-418 in Hagan, J.M., III, and D.W. Johnston, eds. *Ecology and conservation of neotropical migrant landbirds*. Smithsonian Institution Press, Washington, D.C.
- Salthe, S.N. 1985. *Evolving hierarchical systems*. Columbia University Press, New York.
- Sampson, F.B. 1992. Conserving biological diversity in sustainable ecological systems. *Trans. North American Wildl. Nat. Res. Conf.* 57:308-320.
- Sampson, F.B., and F.L. Knopf. 1982. In search of a diversity ethic for wildlife management. *Trans. North American Wildl. Nat. Res. Conf.* 47: 421-431.
- Simberloff, D., and J. Cox. 1987. Consequences and costs of conservation corridors. *Conservation Biology* 1:63-71.
- Smith, R.L. 1990. *Ecology and field biology*, 4th ed. Harper and Row, New York.
- Villard, M.A. 1991. *Spatio-temporal dynamics of forest bird patch populations in agricultural landscapes*. Ph.D. Dissertation, Carleton University, Ottawa, Ontario.

- Villard, M.A., K. Freemark, and G. Merriam. 1992. Metapopulation theory and neotropical migrants in temperate forests: an empirical investigation. Pp. 474-482 in J.M. Hagan, III, and D.W. Johnston, eds. Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C.
- Villard, M.A., P.R. Martin, and C.G. Drummond. 1993. Habitat fragmentation and pairing success in the ovenbird (*Seiurus aurocapillus*). Auk, in press.
- Wiens, J.A. 1983. Avian community ecology: an iconoclastic view. Pp. 355-403 in A.H. Brush and G.A. Clark, Jr. Perspectives in ornithology, Cambridge University Press, Cambridge.
- Wiens, J.A. 1984. On understanding a non-equilibrium world: myth and reality in community patterns and processes. Pp. 439-457 in D.R. Strong, Jr., D. Simberloff, L.G. Abele, and A.B. Thistle. Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton.
- Wiens, J.A. 1989. The ecology of bird communities, Vols. 1 & 2. Cambridge University Press, Cambridge.
- Wilcove, D.S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211-1214.