Book Reviews

A Paradigm in Conservation Biology

Metapopulation Biology. Ecology, Genetics, and Evolution. ILKKA HANSKI and MICHAEL R. GILPIN, Eds. Academic Press, San Diego, 1996. xvi, 512 pp., illus. $89.95 or £65. ISBN 0-12-323445-x.

Metapopulations and Wildlife Conservation. DALE R. McCULLOUGH, Ed. Island Press, Washington, DC, 1996. xii, 429 pp., illus. $55, ISBN 1-55963-457-x; paper, $28, ISBN 1-55963-458-8. Based on a symposium, Albuquerque, NM, Sept. 1994.

Nearly 30 years ago Richard Levins described a theoretical population system in which local populations inhabit discrete habitat patches and have uncorrelated dynamics and high probabilities of extinction but are commonly recolonized. Levins showed that as long as the colonization rate was not less than the extinction rate, the population system would persist. Levins called such a system a metapopulation. Levins's metapopulation concept is strongly related to basic epidemiological models: a patch of suitable habitat is equivalent to the host, colonization is infection, and extinction equates with either recovery or death of the host.

The metapopulation concept might well have languished in the cabinet of academic curiosities had not conservation biologists realized a decade or so ago that human activities, by fragmenting natural habitats, were creating metapopulations from previously continuous populations. Consequently, the metapopulation concept began to replace island biogeographic theory as conservation biology's predominant paradigm. The term "metapopulation" now refers to any system of spatially structured populations, and the Levins model is considered one among many possible variations depending on dispersal rates, persistence probabilities, and the size and spatial arrangement of habitat patches.

These two books provide an excellent overview of the current state of metapopulation studies. Although they deal with the same general topics, their foci are different, and there is relatively little overlap of authors (Jaccard's coefficient of similarity = 0.07). *Metapopulation Biology* concentrates on theory and basic research. The first section begins with a chapter by Hanski and Simberloff on the history and conceptual domain of the metapopulation approach. Harrison and Taylor then provide a taxonomy of metapopulations. "Patchy populations" have extensive movement among habitat patches within a single generation. "Classical" (Levins-type) metapopulations consist of several small and extinction-prone local populations connected by moderate amounts of migration; "mainland-island" metapopulations are made up of one or more large habitat blocks that supply colonists to small, outlying patches; and "non-equilibrium" metapopulations are declining to extinction because dispersal is too infrequent for reestablishment after local extinctions occur. This section ends with a chapter by Wiens linking metapopulation theory with landscape ecology.

Species to which the metapopulation concept has been applied: the Florida scrub jay, mountain sheep, and Steller's sea lion. [Animals Animals; P. Murray, V. McCormick, and S. Moore, respectively]

A section on metapopulation theory and models follows. A variety of metapopulation models now exist, ranging from rather simple incidence-function models that require data only on patch area, pairwise distance between patches, and whether or not patches are occupied to highly sophisticated, spatially realistic simulation models that require data not only on patch size and arrangement but also on patch quality, demography within patches, and observed rates of colonization and extinction. The chapter by Hedrick and Gilpin on genetic effects points out that the genetically effective size of a metapopulation is greatly reduced by high turnover rates and a small number of founders originating from one or a few existing populations. Thus, habitat fragmentation that creates metapopulations out of continuous populations can result in loss of genetic variation.

The next section consists of five papers on metapopulation processes, particularly extinction and dispersal. The buffering effects of dispersal are demonstrated nicely in the paper by Stacey, Johnson, and Taper, who show that a metapopulation of several intermediate-sized populations has a greater probability of persistence than the same number of individuals in a few large but isolated populations.

The last section presents case studies. Thomas and Hanski review the growing literature on butterfly metapopulations. Butterflies seem to provide an ideal model system, since most species utilize one or a very few species of larval host plants, and many of these plants have a patchy structure. Consequently, 75% of British and 60% of Finnish butterflies appear to form metapopulations. Other chapters in this book describe studies on metapopulations of other insects, plants, and small mammals.

Metapopulations and Wildlife Conservation begins with three chapters on theory but then focuses on case studies of species that present real-world conservation challenges resulting from an overall decline of suitable habitat owing to widespread human activities. There are chapters on spotted owls, Stephens's kangaroo rats, Florida scrub jays, monk seals, Steller's sea lions, cougars, grizzly bears, mountain sheep, and tule elk. In some cases fitting a metapopulation model to these organisms seems to be quite a stretch, but the application of metapopulation theory to these species at least has forced the biologists working on them to focus on the spatial arrangement of populations and habitats and to realize that the long-term persistence of many of these species cannot be achieved outside of a metapopulation context.

Though these books do an admirable job of providing an overview of the metapopulation concept in theory and practice, they also hint at some of its deficiencies. Clearly, some species have patchy distributions that seem to fit one or more metapopulation types, and metapopulation models have been useful in developing conservation plans for these species. However, for other species it is difficult to distinguish between habitat and non-habitat, and not all habitat is of equivalently suitable quality. Dealing with such species will require a new generation of metapopulation models, but sufficient data to parameterize these models will be difficult to come by. Though the increasing use of geographic information systems, global positioning devices, and spatial statistics clearly enhances opportunities for obtaining data on the spatial structure of habitats, getting the critical information on local dynamics and dispersal rates at the required level of precision will be a real challenge, particularly in the short time periods that characterize most conservation-planning horizons. Although it is currently fashionable to deal with these issues experimentally, experiments at the appropriate scale are usually impossible, and experimental model systems are unlikely to provide the species-specific information required.

Accurate data on dispersal, the most important unifying process in metapopulation dynamics, are particularly important, but dispersal is very difficult to study. Often hundreds of individuals must be marked and dozens of habitat patches must be searched for dispersing individuals. Moreover, many species exhibit long periods of local isolation with infrequent episodes of long-distance dispersal, requiring a long time horizon for such studies. Additional field time must be spent obtaining long-term data on habitat quality and how it is related to succession and other ecosystem-level processes and on the demography, dispersal, and genetics of the species of interest in several local populations. Each of these presents real logistic and monetary challenges. However, we will be unable to design landscapes that both accommodate human needs and enhance the survival of patchily distributed species until these challenges have been met.

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Assessing Assessments

How Science Takes Stock. A History of Meta-Analysis. MORTON HUNT. Russell Sage Foundation, New York, 1997. xii, 210 pp., illus. $29.95 or £24. ISBN 0-87154-389-3.

In *How Science Takes Stock* Morton Hunt, a journalist, expounds meta-analysis for the general reader. Meta-analysis has been promoted as the best way to summarize a scattered scientific literature on some point. The method, described here as "a means of combining the numerical results of studies with disparate, even conflicting, research methods and findings," is said to enable researchers to "discover the consistencies in a set of seemingly inconsistent findings and to arrive at conclusions more accurate and credible than those presented in any of the primary studies." Meta-analysis most often focuses on assessing or comparing the effects of some characteristic or treatment on some outcome, such as the effect of family background on psychological status or differences between the outcomes of two medical treatments for the same disease. Hunt describes five basic steps in meta-analysis: formulating the problem, collecting the data, evaluating the data, synthesizing the data, and presenting the findings. Meta-analysts have elaborated these steps into substeps that are meant to reduce bias, improve the objectivity of interpretation, and reduce random variation in the results. Though many meta-analyses stop with the description of individual study findings, others—often those with the biggest impact—take a further step to derive a single overarching estimate of the size of the effect under study, with statistical confidence bounds. It is this last step that has raised the most questions and concerns.

Meta-analysis—though Hunt characterizes it as "not itself a science" but "a tool used by scientists"—is said to be not only as precise as available data allow but strictly objective. Thus, shouldn't two meta-analysts with access to the same database make much the same procedural choices and come to similar conclusions? Often they do not. In the wanderings of my own work such cases have not been rare, and I have examined more closely two pairs of meta-analyses that came to sharply conflicting summaries: one pair dealing with the benefits of mammographic screening before age 50 and one with antibiotic treatment of chronic middle-ear effusion. If meta-analysis can come so far from being reproducible, something needs explaining.

The reader of Hunt's book will get little hint of such difficulties, because the extensive literature questioning meta-analysis is scarcely mentioned. Hunt presents one meta-analysis after another as a scientific advance and a triumph of the method, including meta-analyses on such widely different questions as whether violence on TV stimulates antisocial behavior or the accuracy of judgments about the character of a stranger that are formed after only a few seconds of observation. In the few places where Hunt mentions problems they are quickly dismissed. But problems are at the core of the method. They include not only the false appearance of objectivity but consistent bias in the studies selected for analysis, heterogeneity in the effects compared (so that no combined estimate is appropriate), and lack of sufficient knowledge on the part of the meta-analyst to interpret results correctly, especially those coming from a "shop" that does one meta-analysis after another on unrelated topics. For example, some decades of research have shown a sequence of successes in developing new treatments for cancer, but national mortality rates have barely begun to edge downward. Meta-analyses have summarized the study-by-study successes but missed the population-wide failure. (Reasons for this discrepancy are unclear, but may include the selection of the most responsive patients for research study or the choice for study of treatments that require an arsenal of expertise and equipment available only in a tertiary referral center.)

Other difficulties center on the use of the "quality score" that some meta-analysts attach to the studies they review; these are often used to weight studies (for example, a study scored at 50 gets half the weight of the perfect study, scored 100). However, different meta-analysts often score the same studies quite differently. Nor is there reason to believe that the evidentiary value of a study is appropriately scored on a linear scale. Cantekin (personal communication) has shown that in one series of papers nearly every investigator found some benefit from a treatment, but the study scores were strongly and negatively correlated with size of effect, with a downward trend suggesting that the perfect study would find no effect at all. Weighting such studies by quality score diminished the estimated size of the benefit, but only to a small degree.

Other specific problems that I have often seen have come from carelessness (one meta-analysis of a drug effect included a paper on the wrong drug) and from lack of expertise in the subject matter (for example, a meta-analysis of the health risks of chlorination of drinking water (cited by Hunt) came to a result at serious variance with animal studies, which were