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OVERVIEW

LONG-TERM RESEARCH AND THE DYNAMICS OF BIRD POPULATIONS AND COMMUNITIES

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Human activities have dramatically altered the Earth's biosphere and atmosphere during the past few hundred years (Vitousek et al. 1997). Fragmentation and land-use have modified and reduced availability and quality of natural habitat. In addition, greenhouse gasses have modified the capacity of the atmosphere to hold and release heat. Climate variability and change, and land cover and land use change, are key drivers in the dynamics of populations, communities, and ecosystems at multiple spatial and temporal scales (Chapin et al. 1997). Prolonged experimental and observational measurements are now required to adequately address many fundamental ecological and evolutionary questions associated with changes in habitat quality and abundance, increasing amounts of greenhouse gases, and increased climatic variability.

The value of long-term ecological and evolutionary research has been acknowledged repeatedly (Strayer et al. 1986, Likens 1989, Tilman 1989, Cody and Smallwood 1996). Studies on natural selection and population dynamics of Darwin's finches (Grant 1999), interactions among granivore species in desert grassland communities (Ernst and Brown 2001), and biogeochemical fluxes on experimental watersheds at the Hubbard Brook Experimental Forest (Likens 1999) provide ample evidence of the value of sustained, long-term ecological and evolutionary research. Despite their obvious merit, long-term research projects remain relatively uncommon for reasons ranging from size and duration of research awards to constraints imposed by the academic reward system (Gosz 1999). Given the extent of human influence on the global environment, it is imperative that the number of long-term studies in ecology and evolutionary biology be increased. Such studies are needed to document and understand slow processes, rare events, episodic phenomena, processes with high interannual variability, subtle processes, and complex system dynamics, all of which may result from natural and anthropogenic causes (Franklin 1989).

In this overview, I highlight a few of the many contributions made from long-term studies of avian populations and communities. I then briefly discuss long-term research within the context of different research approaches and philosophies. Finally, I describe two research programs at the National Science Foundation (NSF) whose goal is to provide funding to promote and sustain long-term research by investigators at U.S. research institutions. My overall aim is to demonstrate the value of long-term data sets for addressing fundamental questions in ecology and evolutionary biology, as well as for providing management guidance and for informing public policy decisions.

Avian Populations and Communities

Despite the philosophical and monetary constraints on sustaining a long-term research program, extended measurement of population and community dynamics by determined individuals and collaborators has proven invaluable by providing key tests of ecological hypotheses. One critical topic of research is population decline and loss of biodiversity at local and regional scales (Reaka-Kudla et al. 1997). Holmes and Sherry (2001) present an analysis of 30 years of data on breeding-bird abundance and demography in an intact temperate deciduous forest in central New Hampshire. That study serves to illustrate how long-term data can be used to address questions regarding slow, subtle, and variable processes

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of significance to general ecology and conservation of biodiversity. Population changes of breeding birds were measured from 1969 to 1998 in a 10 ha grid at the Hubbard Brook Experimental Forest. Additional measurements were taken from 1986 to 1998 in three other 10 ha grids within the Hubbard Brook Valley. Finally, to determine if local patterns accurately reflected regional patterns of abundance over time, population dynamics across the state of New Hampshire were assessed from 1969 until 1998 using data collected along 22–24 transects as part of the annual U.S. Breeding Bird Survey (BBS).

Holmes and Sherry (2001) found that total number of individuals among all species combined declined nearly 66% over the 30 year period. However, not all species declined in abundance on the 10 ha grid. Of 24 common breeding species, abundances of 12 species decreased significantly over the study period, 9 species remained relatively constant, and only 3 species increased significantly. Thus, changes in total abundance resulted from complex dynamics among multiple species. Annual variation in species abundances was high, thus many years of data were needed to detect with statistical confidence long-term population trends. In several cases, population changes were nonlinear. Abundances of White-breasted Nuthatch (*Sitta carolinensis*) and American Redstart (*Setophaga ruticilla*), for instance, decreased for a period of years and then stabilized. Thus, in some cases, extrapolation from short-term surveys could produce misleading information on long-term population stability or change.

Many of the same population trends noted in the 10 ha grid were observed at the other sample sites, and with the BBS data. In fact, 17 of 24 species had similar trends at the local and regional scales. Such changes conform to the theoretical prediction that local abundance is highly dependent on regional abundance (Ricklefs 1987, Cornell and Lawton 1992). Changes in composition and abundance were linked with successional change in forest vegetation structure, a phenomenon occurring extensively throughout New England (Fuller et al. 1998). Increases in the Black-throated Green Warbler (*Dendroica virens*), for instance, reflect greater abundance of interior forest habitat (Collins 1983). Comparative approaches like that help to illustrate that local patterns reflect regional patterns to a large extent, but that spatial variation for some species or processes may confound extrapolating from local to regional patterns.

The long-term measurement of population dynamics at Hubbard Brook and environs can elucidate patterns of change in species distribution and abundance, but those measurements do not produce direct cause-and-effect relationships. Manipulative experiments coupled with long-term demographic measurements have been used to quantify the role of density dependence in regulating population size of those forest-dwelling birds (Sillett et al. 2000). For the Black-throated Blue Warbler (*Dendroica caerulescens*), in particular, experiments have revealed that suitability of breeding habitat influences population density, age structure, and reproductive output (Holmes et al. 1992, Sillett et al. 2000). Together, those approaches contributed to the development of a new conceptual hypothesis on site-dependent relationships of population size (Rodenhouse et al. 1997). Thus, long-term measurements along with manipulative experiments can document patterns, determine mechanisms, and generate new theories and testable hypotheses.

As noted above, long-term research is needed to document and understand the role of rare and extreme events on population processes. In many cases, such opportunities emerge even though that was not always the original motivation for collecting long-term data. For example, Brown and Brown (1998) used their long-term demographic data set, started in 1982, to explore the potential for rapid evolution following an extreme climatic event in 1996 that resulted in a >50% reduction in a breeding population of Cliff Swallows (*Petrochelidon pyrrhonota*). Following that brief but extreme event, surviving individuals were generally larger with more symmetric bodies than before the event. Thus, that population experienced rapid evolution to a larger body size (Brown and Brown 1998). By continuing their demographic measurements, those investigators can determine if that directional change is persistent or if the population will return to predisturbance conditions because of other selective forces. It is the long-term demographic data that provide quantitative backbone to address those important evolutionary questions associated with rare and extreme events.

Long-term research can help to assess the role of complex processes in population and community dynamics. Martin (1998, 2001) explored relative importance of biotic and abiotic factors on interactions among four ground nesting birds along environmental and microhabitat gradients in central Arizona. Gradients are ideal natural laboratories for revealing broad-scale patterns in species distribution and abundance as environmental parameters change (Smith 1977). Annual abundance of Orange-crowned Warblers (*Vermivora celata*) was positively correlated with May–June precipitation, whereas abundances of Virginia's Warbler (*Vermivora virginiae*) and Gray-headed Junco (*Junco caniceps*) decreased with May–June precipitation. Species also shifted their microhabitat preferences in response to annual changes in precipitation. Those shifts in microhabitat use affected rates of nest-site predation and interspecific interactions. Additional experimental studies elucidated strong asymmetric interactions among some of those species (Martin and Martin 2001). Together, those long-term measurements and experiments demonstrate that this guild of ground-nesting birds experiences complex neighborhood interactions that vary from one year the next.

Methodological Challenges

Over the past 20 years, ecological research has emphasized use of the Popperian approach in which carefully designed short-term experiments are used to isolate variables and test mechanistic hypotheses derived from theory (Hairston 1989). Most experiments are place-based, however, so although detailed local understanding is derived from that approach, some experimental results cannot be extended easily to broader patterns or other systems (Hurlbert 1984). In addition, the short-term nature of most studies (Tilman 1989) may limit their use for ecological forecasting. Nevertheless, the general value of manipulative experiments and inferential statistics in ecological research is indisputable, and they serve as important devices that have helped ecology mature as a scientific discipline (Resetarits and Bernardo 1998).

Clearly, other mechanisms of research are needed to further the knowledge base of ecology and evolutionary biology. Indeed, McIntosh (1987) and Pickett et al. (1994) have called for a pluralistic approach to ecological (and evolutionary) research. Pluralism would include, among other approaches, inductive synthesis, long-term measurement and experiment, modeling, and short-term observational and experimental studies. It will also require a new philosophy that rewards collaboration and data sharing, reflects patience with the generation of long-term data, and abandons the pejorative view that long-term research is merely ''monitoring'' (Taylor 1989).

Although this essay is devoted primarily to expounding on the value and contributions of long-term research, it is well recognized that detailed, short-term studies have provided profound contributions to ecological and evolutionary synthesis. For example, MacArthur's (1958) classic study of niche partitioning in five species of wood warblers was based on 27 to 80 min of observation time spread over two years. That is a relatively short time period even within the life span of a wood warbler. Short-term observations and manipulative experiments, however, are not sufficient to examine the complex issues that now need to be addressed in ecology and evolutionary biology (National Academy of Sciences 2001). Tackling those Grand Challenges will call for sustained, long-term funding, development of new statistical and modeling techniques, and disciplinary integration.

Pattern and cause of changes in species distribution and abundance are of primary interest in basic ecological research. Results from long-term studies addressing fundamental ecological and evolutionary questions, exemplified by Holmes and Sherry (2001) and others, have numerous practical applications, as well. Indeed, comprehensive, long-term observational research, especially when coupled with experiments and modeling, can yield an integrated understanding of cause and effect that may directly inform management and policy decisions. For instance, there is concern over the apparent decline of Neotropical migrants in North America during the breeding season (Maurer and Villard 1996). One potential cause of that decline is habitat fragmentation and its effect on metapopulation dynamics and source–sink relations (Robinson et al. 1995). However, population dynamics models parameterized with observational data have shown that populations can be sustained at regional scales given certain assumptions about source–sink relationships (Donovan and Lamberson 2001). Such information has clear relevance to reserve design, and the conservation and management of biodiversity.

Financial Support for Long-Term Research

Funding agencies, such as the National Science Foundation (NSF), have an obligation to provide support for short- and long-term research by individual investigators and teams of collaborators. Currently most research grants support one or two investigators for three to five years. Sustained funding for long-term research is difficult to acquire. When support exists, it is often insufficient to provide for ongoing data collection and data management needs, plus accommodate the addition of new research activities as opportunities emerge. The NSF's Long-term Ecological Research (LTER) Program is one of the rare examples of sustained funding at the federal level for integrated research in community and ecosystem ecology (Callahan 1984, Franklin et al. 1990). However, LTER research would not be possible without an impressive amount of scientific leadership, cooperation, and collaboration by many members of the research community, and funding and logistical support from other federal, state, and local agencies.

Comprehensive, long-term, site-based research supported by LTER, and other federal and nonfederal sources, has led to influential and controversial contributions to basic ecological theory (e.g. Tilman and Downing 1994), as well as information relevant to conservation and management of natural resources (e.g. the Clean Air Act Amendments of 1990). The LTER program started in 1980 from funding originally provided to NSF to support U.S. participation in the International Biological Program (IBP). The IBP contributed significantly to the maturation of ecological research into ''big science'' (McIntosh 1985). Currently, there are 24 LTER projects in the network on sites ranging from urban ecosystems in Phoenix and Baltimore, to more or less pristine lakes and soils in the Dry Valleys of Antarctica. However, several major ecosystems are not represented in the LTER network, and current limitations on funding prevent adequate support of a broader range of ecological and evolutionary research.

Not all long-term research has or needs the infrastructure and integration to fit into the LTER Program. As a partial remedy, the Division of Environmental Biology (DEB) at NSF, along with the Animal Behavior and Ecological and Evolutionary Physiology Programs in the Division of Integrative Biology and Neuroscience (IBN), support existing long-term projects through the Long-term Research in Environmental Biology (LTREB) Program. The LTREB program was established in the 1980s to provide a modest amount of support to continue an existing, hypothesis-driven, field-based, long-term ecological or evolutionary research project. Funds are provided primarily for supplies, data collection and data management. The projects by Holmes (DEB-0108488), Brown (DEB-0075199), and Martin (DEB-9707598) described above have received or currently receive LTREB support. More information on the LTREB Program can be found at http://www.nsf.gov/bio/progdes/ltreb.htm.

Summary

Ecological systems are widely recognized to be highly dynamic in response to natural or anthropogenic disturbances (Pickett and White 1985, White and Jentsch 2001, Wu and Loucks 1995). Even in the absence of disturbance, relatively mature ecological systems can exhibit tremendous spatial and temporal variability (Collins 2000). Only long-term studies, such as that by Holmes and Sherry (2001), combined with carefully documented and preserved data sets (Michener et al. 1997), will provide the context and background for describing those patterns and understanding the nature of change over time. Such understanding leads to hypothesis development, and the design and implementation of manipulative experiments to identify the various mechanisms that drive spatial and temporal change in populations, communities and ecosystems. A pluralistic approach will be essential to addressing the considerable ecological challenges ahead in response to global environmental change.

Long-term research will serve a key role in tackling those multifaceted challenges.

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