Modeling the Distribution and Abundance of Monarch Butterflies

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THE COMPLEXITY OF THE MONARCHS’ ANNUAL CYCLE

Monarch butterflies utilize diverse habitats spanning most of temperate North America during their annual migratory cycle, and populations fluctuate dramatically within and between years. In the course of an annual cycle—which includes breeding in the United States and southern Canada, migrating over a broad latitudinal range, and overwintering in central Mexico and coastal California—monarchs exhibit micro-scale movement as foraging larvae; meso-scale movement as foraging, breeding, and overwintering adults; and macro-scale movement as adult migrants (Ackery and Vane-Wright 1984; Vane-Wright 1993). During each of these stages, the distribution and abundance of monarchs are affected by both current environmental conditions and events that occurred during preceding stages. For example, the numbers of monarchs in Minnesota in June may be affected by weather conditions in Texas during April and May, since these monarchs probably spent their egg, larva, pupa, and early adult stages far south of Minnesota. A late freeze in Minnesota (not unheard of in June!) will also affect monarch populations, as will monarch or milkweed diseases, other milkweed-consuming herbivores, and monarch predators. In addition to these natural factors, monarch populations are vulnerable to land use change (Malcolm and Zalucki 1993; Hoth et al. 1999) and, owing to their susceptibility to temperature extremes, human-induced climatic change (Rawlins and Lederhouse 1981; Zalucki 1982; Malcolm et al. 1987; Zalucki and Rochester 1999; York and Oberhauser 2002).

These factors require that the study of monarch populations involve a large range of temporal and spatial scales, and a variety of research approaches including laboratory, field, and mathematical studies. The first three sections of this book presented results of empirical studies conducted in the laboratory and the field. These studies were designed to document, and in some cases explain, how monarchs interact with their environment throughout their annual cycle of breeding, migrating, and overwintering. In this section, we present chapters that have combined empirical data with mathematical models to further our understanding of the population dynamics of monarchs.

ECOLOGICAL MODELS

The study of ecology involves trying to understand the interactions of many systems and environments, and these interactions are often too complex to understand simply by documenting patterns and following our intuition about the causes of these patterns. When this is the case, a clear analysis requires a simple and explicit mathematical presentation. Ecologists use mathematical models to help understand the complex patterns and processes that link all of the parts of ecological systems. While models almost always involve intentional simplifications of ecological patterns, they force us to state clearly our assumptions about these patterns and...
their causes and consequences. They can be used to tell us what could happen in a system given changes in the living or nonliving environment, what factors are likely to be most important in causing observed patterns, and in some cases, what else we need to know to better understand the patterns we observe.

Scientists have used mathematical models to explain ecological patterns since the eighteenth century, although early modeling focused on human populations. In his essay on population, Malthus (1798) used simple mathematics to show that although numbers of organisms can increase exponentially (e.g., 1, 2, 4, 8, 16, . . .), their food supply is unlikely to do the same. Thus, he reasoned that reproduction must eventually be checked by food supply. This kind of mathematical reasoning spawned an interest in the study of population growth rates. Other early models looked at relationships between organisms; pioneering work by Ross (1908, 1911) used mathematical models to explain the propagation of malaria in mosquitoes and humans. Malthus, Ross, and others made explicit assumptions about how important features of the environment interacted, and then constructed mathematical equations to model these interactions.

The science of ecology is advanced by a better understanding of the ways in which organisms interact with their environment. Mathematical modeling is one methodology for precisely defining such interactions and for defining relationships that can be tested against observed data. Thus the relationships defined by ecological models have both basic and applied importance. From an applied perspective, models allow us to test hypotheses related to the impact of various factors on population dynamics. For example, we could use models to assess the potential effect of anthropogenic changes in land use and agricultural practices on monarch populations, or to predict potential impacts of future changes in climate. Models can help identify factors that affect monarchs during each period of their annual cycle, and additional research required for a more complete understanding of the population dynamics of these butterflies. Understanding these factors will benefit policy makers concerned with conservation, members of the public with an interest in monarch biology and conservation, and industries whose activities may affect monarch populations.

**POPULATION MODELS**

Chapter 25 by Altizer and colleagues follows the work of Malthus and other ecologists who model how populations change over time. Altizer and coworkers studied a protozoan parasite called *Ophryocystis elektroscirrha* that has negative effects on the fitness of monarchs (Altizer and Oberhauser 1999) and is usually transmitted from mothers to their offspring. Theory predicts that parasites that are only transmitted from mothers to offspring should not harm their hosts, since their success depends on the reproductive success of these hosts. The researchers combined empirical work (measuring the rates of transmission of *O. elektroscirrha* from male and female monarchs to their offspring) and mathematical modeling to understand the factors that might allow this parasite to persist in monarch populations. The chapter represents an exciting combination of lab, field, and mathematical work to understand basic questions about monarch populations, and is an important contribution to our understanding of disease dynamics in general. The model is clearly a simplification; in a natural environment, a multitude of factors will play an important role in determining abundance. However, this study helps us to understand how *O. elektroscirrha* can have negative consequences on fitness and still persist in monarch populations, and how the parasite might affect the abundance of monarchs.

Whereas Chapter 24 helps us to understand abundance, the other two chapters in this section focus on the distribution of monarchs. Zalucki and Rochester, and Feddema and coauthors use knowledge of monarch growth and development, flight speeds, and weather patterns over large scales to indicate where and when monarchs are expected to occur. Zalucki and Rochester’s model (Chapter 26) predicts the effects of weather and arrival times of monarchs from Mexico on the timing and synchrony of spring and summer generations. The model incorporates data collected by many researchers on monarch development under different climatic conditions, arrival times at different locations, and temperature conditions that are lethal to monarchs. By simulating monarch development throughout the North American range using data from hundreds of weather stations, the model predicts the proportion of the monarch population that
is in each life stage at each location throughout the season. Not surprisingly, the model suggests that climate should have an important influence on the distribution of monarchs, with large differences in the timing of the relative abundance of different monarch stages across years and space. Zalucki and Rochester used actual data to test the model and found that it correctly predicted the timing of monarch generations across several years. While factors such as the abundance and density of milkweed and the presence of predators will also affect monarch numbers, by narrowing the scope of the model to weather alone, Zalucki and Rochester are able to make simple predictions about the likely exposure of monarchs to potential risks such as those imposed by changes in agricultural practices.

Whereas Rochester and Zalucki model when and where monarchs are expected to occur based on local conditions, Feddema and coworkers (Chapter 27) model monarch movement explicitly. They simulated spring and fall migration, using information on when and whether monarchs leave and arrive at given locations as a function of meteorological and seasonal conditions. In addition to simulating movement, the model predicts the number of generations that are produced each year, based on temperature. Users can input many parameters, such as the daily distance traveled by monarchs as they migrate, the number of degree-days required for each stage of development, and the number of days that female monarchs lay eggs. By varying the value of each parameter and observing the sensitivity of the model’s output to this variation, we can learn which features might be most important in determining the distribution and abundance of these butterflies. The inclusion of so many parameters in the model helps us to understand how several environmental factors affect population dynamics, and provides more realism than simpler models that include only a few features of the environment. A potential drawback of this complexity is that the effects of one parameter may depend on the values of other parameters.

Real data are important to ecological models. Data collected in both field and laboratory studies allow us to use realistic values in our models, and also to test model output. Of particular note in models of monarch distribution is the use of data collected by volunteer citizen scientists. Monarch Watch (Taylor 1999; Monarch Watch 2002), Texas Monarch Watch (Calvert and Wagner 1999), Journey North (Journey North 2002; Howard and Davis, this volume), and the Monarch Larva Monitoring Project (Monarch Larva Monitoring Project 2002; Prysby and Oberhauser, this volume) all involve members of the public in long-term, large-scale data collection efforts, and result in data that will continue to allow us to develop realistic models and provide a means to test their validity.

Modeling monarch populations is an important exercise, and the models presented here represent an exciting beginning. More comprehensive models of the population dynamics of monarchs over large spatial and temporal scales are possible, and we hope that future models incorporate their biology and ecology; the phenology, abundance, and distribution of milkweed; the dynamics of vegetation; and climate. These models will be interesting for their own sake, but will be of paramount importance in gauging the impact of biotic and abiotic influences, including patterns of land use and anthropogenic climate change, on the stability of monarch populations.

References


