

## Demography of Songbird Populations in a Rapidly Changing World: The Importance of Long-Term Studies

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### ABSTRACT

A major goal of ecological research is to understand how ecological factors, such as food and predator abundance, interact to shape birth and death rates. Case studies describing this research can provide students with an understanding of how ecological conditions affect demographic rates, as well as an opportunity to explore and interpret real data. We have developed a Web-based teaching module based on a long-term study of a migratory songbird, the black-throated blue warbler (*Dendroica caerulescens*). The website describes this species and the ecological factors that affect its population growth and provides three exercises developed to span a range of student levels.

**Key Words:** Population ecology; density dependence; climate change; online module.

### ○ Background on Study

Black-throated blue warblers (*Dendroica caerulescens*) have been studied intensively at the Hubbard Brook Experimental Forest in New Hampshire since 1986 (for information on education and outreach programs, visit <http://hubbardbrookfoundation.org/overview/>). A primary goal of the study has been to identify factors that limit populations of migratory birds and to determine how conditions during the breeding, wintering, and migratory stages interact to affect demographic rates (Sillett et al., 2000; Holmes, 2007). This research documented that warblers had higher reproductive success in years with a higher abundance of caterpillars, their primary food, and in years with fewer squirrels and chipmunks, their major nest predators (Nagy & Holmes 2004, 2005). In addition, in years with a higher number of breeding pairs in the study area, the average number of young produced by each pair was lower, demonstrating that the population is regulated by density dependence (Rodenhouse et al., 2003). Collectively, these data show that the reproductive success of black-throated blue warblers depends on multiple ecological factors, providing a real-life

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example of how populations are interconnected with populations of their prey and predators.

The warbler study also highlights the importance of long-term data for designing effective conservation strategies, which will require predicting how climate change could influence population dynamics and interactions between species (Crick, 2004). In a comparison of three sites along an elevational gradient, warbler reproductive success was greatest at the high-elevation site, which had relatively high food abundance and few nest predators (Rodenhouse et al., 2003). However, climate models predict that the flora and fauna that now characterize lower-elevation forests will replace current high-elevation habitats (Rodenhouse et al., 2008). The warblers may therefore lose their most suitable habitat, providing an example of how climate change can affect a wildlife population via changes in the abundance of predator and prey species.

### ○ Module Contents & Organization

We have developed a Web-based teaching module (<http://btbw.hubbardbrookfoundation.org/>) based on the long-term demographic study of black-throated blue warblers, with the goal of teaching fundamental concepts in population ecology while leading students through the methods and findings of an ongoing study. The website is organized into four sections (background, warbler biology, methods, and results) followed by assignments; each section is composed of multiple webpages containing explanatory text, pictures, videos, and graphs. Here, we provide a brief overview of each section of the module.

In the background section, we explain the value of demographic studies, which allow scientists to assess whether a population is increasing, declining, or stable. We introduce the concept of reproductive success, defined as the average number of young produced by each breeding pair in the population. We then focus on three ecological factors – nest predation, food, and breeding density – and

explain how each factor is expected to affect warbler reproductive success. The warbler biology section summarizes the annual cycle of a migratory bird and describes warbler breeding ecology. The methods section provides an overview of the study site and the field methods used to measure warbler demography and our focal ecological variables.

In the results section, we graphically highlight the major findings of the long-term study. We show how average annual reproductive success has varied between years, and explain this variation by relating reproductive success to each of our focal ecological variables (see example in Figure 1). We also discuss the conservation implications of this research, highlighting how climate change may decrease the amount of habitat in which birds produce the most young.

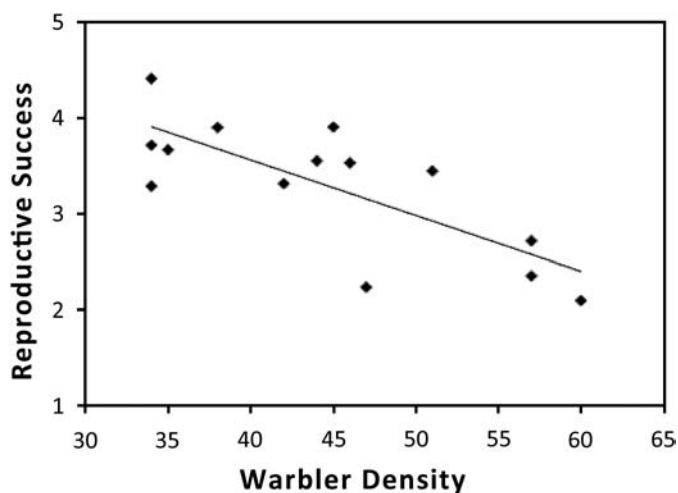
## ○ Exercises & Classroom Implementation

We provide three assignments, each intended for students at different levels and to emphasize different aspects of the research. Answer keys and information on how the assignments conform to educational standards outlined by the National Research Council (1996) are available to teachers on a password-protected page (password requests can be directed to [jwilson@hbresearchfoundation.org](mailto:jwilson@hbresearchfoundation.org)). We also provide a link where teachers can comment on the module, provide implementation suggestions for other teachers, or contribute additional assignment questions.

The first assignment (labeled A on the website) is a set of short-answer questions designed to assess comprehension and to confirm that students have read the Web-based material. Questions focus on demography, the ecological factors affecting reproductive success, and the potential effects of climate change on the study population. These questions could be used as part of an in-class discussion or as homework and would be appropriate for students at the middle or high school level.

The second assignment (B) emphasizes the importance of collecting long-term demographic data while teaching data interpretation and graphing skills. We provide a downloadable Microsoft Excel data set and directions for how to make graphs in Excel. Students are asked to graph the relationship between food availability and reproductive success over subsets of the study period and evaluate whether a shorter study would have led to the same conclusions. The graphs show that over some, but not all, time intervals, the pattern is similar to that of the complete study, highlighting the value of long-term data. The second half of this assignment provides students with an intuitive understanding of how ecological factors interact by asking whether nest predator abundance can explain deviations from the expected relationship between food abundance and reproductive success. We show that in some years, reproductive success is higher or lower than expected given the food abundance (i.e., these points are far from the line), and ask the students to predict the relative size of the nest predator population in those years and then graph the nest predation data to test their hypotheses. For younger students, this assignment could be done in groups as an in-class exercise, while the whole assignment, or the more advanced second half, would be appropriate for high school and introductory undergraduate courses.

In the final assignment (C), we present a simulation that demonstrates how nest predators, food, warbler density, and the strength of density-dependent competition can interact to determine warbler population size. Each of these factors is represented as a variable that students can adjust using built-in sliding scales. Increasing the number of predators or decreasing the amount of food leads to lower population sizes. The strength of density dependence is defined as the decline in reproductive success per individual as one more



**Figure 1.** The reproductive success (average number of young produced per territory) of black-throated blue warblers was negatively correlated with warbler density (individuals per 64 ha). Data were collected from 1986 to 1999; each point represents an annual average for all territories in the study population.

individual is added to the population; setting the value of this variable to zero results in exponential population growth. Other combinations of ecological variables bring the population to its carrying capacity, which is determined by the food, predator, and density dependence settings. The assignment provides additional background material and exercises that encourage students to develop hypotheses and model population trajectories under different ecological conditions. This conceptual introduction to density dependence would be appropriate for high school and undergraduate biology and ecology courses. The simulation was developed using NetLogo (Wilensky, 1999) and requires Java, which can be downloaded free at <http://www.java.com>.

## ○ Conclusions

Successful science courses must keep students engaged while teaching abstract concepts, methods of scientific inquiry, and critical-thinking skills. Research has shown that students learn and retain information more effectively when concepts (e.g., density dependence) are paired with active learning experiences that emphasize the process of science (Handelsman et al., 2004). These can include tangible examples of scientific investigations and opportunities for students to develop their own hypotheses, to collect and manipulate data, and to interpret results. These activities engage students in the scientific process and help them develop the critical-thinking skills necessary to evaluate the results of scientific investigations (Wood, 2009). Our online learning module aims to teach fundamental concepts in population ecology by leading students through the methods and conclusions of an ongoing demographic study, while providing an opportunity to analyze and interpret real data. Ultimately, we hope that this module will provide students with a deeper understanding of population ecology and a greater appreciation of the scientific method.

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