Special feature

#### Population dynamics of forest-defoliating insects

Andrew Liebhold - Naoto Kamata

#### INTRODUCTION

# Are population cycles and spatial synchrony a universal characteristic of forest insect populations?

Received: April 25, 2000 / Accepted: September 22, 2000

Abstract Foliage-feeding forest insects have served as model systems in the study of animal populations for more than 50 years. Early studies emphasized identification of "key" mortality agents or density-dependent sources of mortality. However, these efforts became burdened by rhetorical ambiguity, and population ecologists are increasingly focusing on characterizing population behavior and identifying the processes that generate that behavior. Two types of behavior seem to be common in forest insect populations: periodic oscillations ("population cycles") and spatial synchrony (synchronous fluctuations over large geographic areas). Several population processes (e.g., hostpathogen interactions) have been demonstrated to be capable of producing periodic oscillations, but the precise identity of these processes remains uncertain for most forest insects and presents a challenge to future research. As part of these efforts, a greater emphasis is needed on the use of statistical methods for detecting periodic behavior and for identifying other types of population behavior (e.g., equilibrium dynamics, limit cycles, transient dynamics). Spatial synchrony appears to be even more ubiquitous in forest insect populations. Dispersal and regional stochasticity ("Moran effect") have been shown to be capable of producing synchrony, but again more research is needed to determine the relative contribution of these processes to synchrony observed in natural populations. In addition, there is a need to search for other types of time-space patterns (e.g., traveling waves, spiral waves) in forest insect populations and to determine their causes.

Key words Population dynamics · Periodic oscillations · Outbreak · Nonlinear dynamics

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#### Introduction

Royama (1992) states that the ultimate question in population dynamics is "Why do animal populations fluctuate as they do?" Throughout the twentieth century, foliage-feeding forest insects have served well as model systems for answering this question. Most of these insects exist in habitats that are relatively free of anthropogenic disturbance and thus lend themselves as suitable subjects for long-term studies. Long-time series are the "bread and butter" in the field of population dynamics because many dynamic patterns only become evident after 20 or more years of data collection. Foliage-feeding forest insects are also valuable model systems because they are relatively easy to sample and the habitat is rarely destroyed by their feeding, even during outbreaks.

The seven papers in this special feature present syntheses of the current knowledge on the population dynamics of some of the most widely studied foliage-feeding insects. If these papers are contrasted with earlier studies of forest insect dynamics over the past several decades, it becomes clear that during this period there has been an evolution of approaches to the field of animal population ecology. The objective has always been to elucidate the mechanisms behind the dynamics of selected species, but the specific questions have varied.

Early scientists (e.g., Varley and Gradwell 1960; Morris 1963) focused on identifying the most "important" factors responsible for changes in population density. The approach most commonly taken was to collect life table data and apply specialized statistical procedures (e.g., "keyfactor analysis"; Varley and Gradwell 1960) to identify specific causes of mortality that explained the largest portion of variation in change in density. Although great advances were made by this work, this approach is rarely applied in contemporary studies because of the ultimately nebulous definition of what makes a certain type of mortality "important" (Royama 1996).

As these efforts tapered off, an increasing emphasis was placed on identifying the existence and causes of population

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