Chapter 1
Insects and the Ecological Basis for Mathematical Modelling

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Abstract This book brings together nine chapters that aim to present the most recent research on the interface between ecological modelling and entomology. The chapters are summaries of research performed in different Brazilian institutions, UK and Ireland universities. The idea of the book is to present different focuses of study by aggregating theoretical ecology and applications in agricultural and medical entomology, also emphasising pest management and conservation. This chapter briefly summarises a history of the population theory applied to entomology and will introduce the reader to the topics developed in the following chapters.

Keywords Entomology • Insect population modelling

1.1 Introduction

Insects are fascinating organisms that have suffered evolutionary adaptations over geologic periods. Their extraordinary stages of evolution have provided them with special characteristics to occupy different habitats and to face a variety of environmental conditions (Carpenter 1953). Due to this flexibility, insects have been able to develop specific abilities and strategies for exploiting resources to guarantee their survival even in adverse conditions. They are advantageous to humans in various contexts. For example, there are insect species that act as natural enemies of pests, that yield products beneficial to humans, such as the honey bee and silkworm, and that can be used as forensic indicators, biotherapy and food (Goldsmith et al. 2005; Parnés and Lagan 2007; Wells and Stevens 2008; Srinivasan 2010; van Huis 2012). However, although these organisms exhibit interesting mechanisms of

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© Springer International Publishing Switzerland 2014
C.P. Ferreira, W.A.C. Godoy (eds.), *Ecological Modelling Applied to Entomology*, Entomology in Focus 1, DOI 10.1007/978-3-319-06877-0_1

adaptation that have important ecological roles and are beneficial for humans, they have also displayed a high capacity for increasing their population sizes, mainly in systems with a high food availability, such as forests, crops, terrestrial and aquatic environments, or even animal hosts. A high density of insects could severely damage growing crops and cause epidemics, host infestations and a trophic imbalance with negative consequences for conservation (Lima et al. 2009).

1.2 Insects and Their Evolutionary Strategies

Evolutionary strategies in insects have been classified according to the bioecological characteristics, which involve relevant factors such as body size, egg size, development rate, fecundity, longevity, sex ratio, dispersal ability and density dependence (Speight et al. 2008). These strategies could be understood as responses to evolutionary pressures to attain the best species performance and involves striking a balance between costs and benefits (Harrison et al. 2010). The best performance usually involves a high magnitude of fecundity (Awmack and Leather 2002) which is mediated nevertheless by density-dependent mechanisms. This observation could be understood as optimisation, ecologically expressed by r- or K-strategy. This is a theory that describes different strategies by combining traits in an attempt to obtain the best advantage by confronting parental investment and the quantity and quality of offspring (Pianka 1970). Generally, species governed by r-selection invest in many offspring, whereas k-strategists focus theirs on a few (Pianka 1970). Conversely, r-selected insect populations are unpredictable in their ecological trends, where the cycles they experience over time depend on the demographic parameters of fecundity and survival. Occasionally, an overexploitation of resources will encourage populations to invade new areas (Davis et al. 2005). Insects viewed as k-strategists are frequently regulated by density-dependent factors and have a low fecundity (Matthews and Matthews 1978).

The movement of insects among different areas may be viewed according to different perspectives and perhaps more appropriately classified into two basic types: passive and active (Yates and Boyce 2012). The passive type has highlighted the need for studies that emphasise phytogeography history, demography and population dynamics mainly due to changing dynamic patterns in human movement (Jones 2001; Bentley et al. 2012; Fresia et al. 2013). The benefits of modern transportation, the economic growth of emerging countries and globalisation have facilitated the transport of several items for human consumption, including organic products, such as seeds, seedlings, cereal, fruits, meat, and many others (Bentley et al. 2012; Hu et al. 2013). In response to this increasing transport of items, several pest species have invaded new areas and frequently cause problems for the new environments or hosts (Mazzi and Dorn 2012).

1.3 Insects and the Climate Changes

Global warming has also exerted a significant influence on the distribution of species around the world, with negative impacts on conservation, agriculture and public health (Ferron and Deguine 2005; Kiritani 2006; Andrew and Hughes 2007). Noticeably, insect species living in areas with predominantly high temperatures are stimulated to leave their origin regions to new areas, with similar temperatures, that were previously not inhabited by these species (Ammunet et al. 2011). The implications of climate change for people and the environment are unpredictable, but the dynamics of diseases transmitted by insects is a relevant concern that is shared among nations worldwide. Malaria afflicts more than a billion of people and causes 2 million deaths per year (WHO 2011a, b). Dengue fever infects 100 million people annually (WHO 2011a). Vector mosquitoes have developed a significant resistance to insecticides, which decreases the efficiency of the methods used to control these disease vectors (Zaim and Guillet 2002). All of these factors underscore serious concerns about the future of global public health.

1.4 Insects and Their Responses

Resistance to insecticides is an increasing challenge currently faced by chemical manufacturers. The use of chemical products without criteria, as well as the widespread use of insecticides throughout the world, has increased the resistance to different product classes (Carvalho et al. 2013). New chemical formulations have been proposed as an attempt to increase the efficiency of products (Casida and Durkin 2013). However, product toxicity for the environment, animals and humans is a serious consequence for social welfare in addition to the high costs for growers (Isman 2006). Transgenic crops represent a part of the modern agricultural strategy to combat pest attacks (Kos et al. 2009) and consist of plants that are genetically engineered to produce insecticidal proteins encoded by *Bacillus thuringiensis* (Bt) genes (Shelton et al. 2002). More Bt crops are employed worldwide today than 15 years ago and are housed on more than 420 million hectares (Tabashnik et al. 2013). These observations are interesting, but their implications for an invasion of secondary pests over time remains to be evaluated (Qiu 2010). Perhaps the greatest challenge for the coming decades is to reconcile the rising needs of the fight against vector-borne disease and devastating agricultural pests with biological conservation. This would open new perspectives for optimising technology and various strategies to appropriately apply modern synthetic insecticides, biological control agents, botanical insecticides, pheromones, insect growth regulators, genetic manipulation of pest species, host-plant resistance, and cultural techniques for organic farming and intercropping (Kogan and Jepson 2007; Thacker 2002).

1.5 Insects and the Numbers

The population pest density frequently reaches outbreak levels that pose considerable economic and environmental impacts to agriculture, forests and to human health around the world (Perveen 2012). Much of the variability in insect pest population density may be attributed to several density-dependent or independent mechanisms, including interacting effects with weather or natural enemies (Bommarco et al. 2007). Despite the considerable number of recent studies on ecology and population dynamics in insects (Liebhold and Tobin 2008), more quantitative and qualitative information is required to generate different possible analytical approaches. Empirical approaches may increase the knowledge about ecological patterns implicit in population dynamics of pest species and create a database of proposed strategies for control that consider the risks arising from the previously mentioned factors (Ives and Schellhorn 2011).

Dealing with quantitative data requires appropriate analytical tools that come mainly from computation, mathematics and statistics. Ecological modelling is an essential part of both research and management of pest insects and is the major tool for predicting population dynamics. The history of mathematical modelling in insects begins with the conventional steps that exist for biological scenarios, i.e., abstraction and subsequent proposition of theoretical models, which, although considered simple, are capable of retaining the most important ingredients of population change (Murray 2001). Models of this nature, which have existed for more than a century, express mathematical functions capable of describing the shape of the ecological patterns of time series, such as the paper by Benjamin Gompertz that emphasises the law of human mortality (Gompertz 1825). Simple models, such as the Verhulst model (Verhulst 1838) for population growth, have bolstered more sophisticated formulations, which have improved by adding important mechanisms that make the model more realistic by including delayed density-dependence, interspecific and trophic interactions, age or stage structure, spatial dimension, stochasticity and control strategies (Bascompte and Sole 1998; Murray 2001; Lima et al. 2009; Rosenheim 2011).

1.6 Insects and Their Interactions

The structure of insect populations and communities includes complex relationships that express different types of interactions, such as intra and interspecific competition, cannibalism, predation, parasitism, commensalism, and a variety of relationships with the environment (Felton and Tumlinson 2008; Polis 1991). On one hand, modelling insect populations is a challenge because life cycles are complex and involve lags that produce a strong dependence between life stages mainly in species that exhibit non-overlapping generations (Hassell et al. 1976). On the other hand, there are species that overlap generations, and thus, the systems exhibit reproductive patterns similar to mammals. In both cases, two different types of equations are required to describe the system dynamics: one for non-overlapping populations and one for overlapping populations (Edelstein-Keshet 1978). However, insect life cycles are shorter than those of vertebrates or even perennial plants, and some of them are easily reared in the laboratory, which encourages experimentation and mathematical modelling (Cushing et al. 2003).

1.7 Insects and the Models

Verhulst (1838), Thompson (1924), Lotka (1925) and Volterra (1926) are the precursors of ecological theory, which was the basis for the first mathematical models presented to study populations and interactions between species of arthropods (Hassel 1978). Subsequently, Nicholson (1933) and Nicholson and Bailey (1935) proposed the first models to investigate prey-predator interactions, which served as a great foundation for host-parasitoid models. The studies performed by Nicholson (1954, 1957) provided long-term laboratory series that focused on the population dynamics of *Lucilia cuprina* (Diptera: Calliphoridae) to investigate effects of resource scarcity at different life stages. The results obtained described a series with quasi-cycles and have been widely revisited by ecologists, such as the paper by Gurney et al. (1980) entitled "Nicholson's blowflies revisited".

In 1985, Prout and McChesney (1985) published an interesting and useful discrete time mathematical formulation that considered the delay effect on fecundity and survival of competition during the larval stage of *Drosophila melanogaster* to demonstrate how the functions of larval density, fecundity and survival can influence the dynamic behaviour of populations in the laboratory (Prout and McChesney 1985). This theory has been widely used to model blowfly populations in a biological invasion scenario (Serra et al. 2007; Coutinho et al. 2012; Moretti et al. 2013).

James Carey (1993) provided an extremely important contribution for the application of statistics and ecological theory to entomology. Carey presented important demographic methods to study life tables in insect populations. Dennis et al. (1995) initiated an era of notable papers by proposing the LPA model, which is designed to combine theory and experimentation to investigate ecological equilibrium patterns in *Tribolium castaneum* by considering different life stages, such as larva, pupa and adult. A textbook entitled "Chaos in ecology: experimental nonlinear dynamics" is a nice compilation of the mechanisms of population growth, nonlinear stage-structured population models, and chaos in ecology.

1.8 This Book

In the current book, we present a compilation of studies that are at the interface between mathematical modelling and entomology. Our proposal presents models constructed to study different types of insects in distinct habitats and scenarios to demonstrate how the theory can be used as a powerful tool to describe ecological patterns and project tendencies. The next eight chapters will present an overview of different ecological modelling applications, emphasising agricultural, medical entomology and conservation.

The chapters describe a synthesis of the most recent research developed in several Brazilian research institutions and also in three universities in the United Kingdom and Ireland. A spatially explicit model is presented in Chap. 2 that assumes density-dependent effects during pre- and post-dispersal in a host-parasitoid system. The model reveals that behaviour may influence the spatial distribution and the abundance of species in the landscape. Chapters 3 and 4 focus on how abiotic factors affect the life cycle and population dynamics of mosquitoes with consequences for dengue transmission. Chapter 3 presents a mathematical model to evaluate parameters dependent on temperature and that are significantly influenced by rainfall. The model assumes that seasonality causes the varying population size and simulates a coupling of mosquitoes and humans to assess the transmission of dengue virus. In the fourth chapter, a mathematical model describes the influences of temperature on *A. aegypti* life stages by characterising transitions and death rates as a function of temperature. With this formalism, they also describe the influence of the temperature on dengue transmission.

In the fifth chapter, metacommunity models are used to investigate the geometry of riverine networks, emphasising aquatic insects. The authors show that the strength of the environmental impact, the spatial position of the impact within the network and the degree of dispersal among local communities can severely affect the performance of statistical models regularly employed in biomonitoring programs. Chapter 6 provides insights into how to represent trophic interactions by using different models that consider semelparity and iteroparity and demonstrate the relevance of the interaction strength in determining food web dynamics. Chapter 7 presents coupled map lattices to study the spatio-temporal insect dynamics. The lattices consider natural degradation as well as dynamics affected by chemical substances or volatiles that move by diffusion and advection due to the wind. The proposal to use coupled map lattices aimed to analyse the effects of the insect behavioural response on their density, distribution and persistence. Chapter 8 proposes an important strategy for pest management programs by presenting a mathematical formalism for monitoring pest abundance in agricultural fields. A mathematical background for methods of numerical integration is provided and application of numerical integration in the pest monitoring procedure is discussed to demonstrate this proposal. The ninth chapter delineates how to model overdispersed data in typical entomological scenarios, mainly when outcomes of interest are in the form of counts or proportions. As a foundation for the model, the authors discuss possible causes for overdispersion in insects and use different approaches to analyse distinct ecological patterns of distribution.

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