Insect population ecology in British Columbia

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The heydays of population ecology in British Columbia occurred during the 1970s and 1980s. Significant work was conducted by many people, and at several institutions, including: the University of British Columbia; Institute of Animal Resource Ecology; Simon Fraser University; Agriculture Canada, Vancouver Research Station; and the Canadian Forest Service, Pacific Forestry Centre. This paper reviews some of the work, from the viewpoint of the authors. The first section relates to agricultural insects and the second focuses on forest Lepidoptera in BC.

Population ecology of agricultural insects

Many researchers in BC have studied various aspects of population ecology. Rather than list these people and their contributions, this section focuses on the work of one research group – allowing detailed development of a story. The group was selected because it treated population ecology as a subject in its own right. This approach to ecological studies was prevalent in the 1960s-1980s, and is quite distinct from the approach that currently dominates, in which commercial problems drive much of the research. The title of this section reflects the current approach; the group being considered took quite a different view.

The research group consisted of Neil Gilbert (Associate Professor, Institute of Animal Resource Ecology), Andrew Gutierrez (Visiting Professor from Purdue University; later Professor, University of California, Berkeley), Bryan Frazer (Research Scientist, Agriculture Canada, Vancouver Research Station), post-doctoral fellows Rhonda Jones and Penny Ives, University of British Columbia graduate students, and summer students.

The researchers selected organisms with characteristics that facilitated quantitative study of ecological relationships. They then used a reductionist approach, quantitatively defining relationships and processes at lower scales and combining those quantitative relations in simulation models to explain population trends (Gilbert *et al.* 1976). A characteristic of the work was the constant interplay between experiments in the laboratory, sampling, observations and experiments in the field, and modeling, to achieve a realistic, dynamic picture of natural systems. The approach was logical, it worked, and it still applies today. However, the book, Gilbert *et al.* (1976) met with considerable criticism (Lawton 1977), largely because it took to task current and past approaches to population ecology. In particular, Gilbert *et al.* (1976) objected to ecological studies that focused on the organism rather than underlying ecological relationships that can be generalized among organisms. They also objected to laboratory-centred population ecology and theoretical approaches that are not tested under field conditions.

One of the first organisms selected by the group was the aphid *Masonaphis maxima* (Mason) (Frazer and Forbes 1968). This is a single-host aphid that appears on thimbleberry in sheltered locations in April, goes through 3-5 generations parthenogenically depending on plant quality and weather, and produces overwintering eggs in July. Because a special morph is needed to produce sexuals, and sexuals are necessary to obtain eggs, the aphid must be able to respond to changes in plant quality two generations in advance. A very good understanding of the population dynamics of the aphid has been achieved (Gilbert and Gutierrez 1973; Gilbert 1980), and the work - based on this non-commercial system - provided the seeds for many of the applied results obtained by Andrew Gutierrez and co-workers on cotton, coffee, alfalfa, cassava and other crops (e.g. Gutierrez and Baumgärtner 1984). In addition, the aphid, due to a peculiarity in its life cycle, provides a convincing proof for one function of sex. Sex is required to maintain dimorphic fundatrix aphids (Gilbert and Raworth 1998), and the dimorphism, a differential production of sexual forms at the end of the season, adapts the aphid to its heterogeneous and unpredictable environment. This is as yet, the only proven function for sex.

Movement is a key element in the population dynamics of an insect. To study movement, the group, which included Rhonda Jones, Michael Guppy and Vince Nealis chose to study the cabbage butterfly, *Pieris rapae* (L.) (Jones 1977). Rules were obtained for short-distance movement, and these rules were then used to predict long-distance movement (Jones *et al.* 1980). The butterfly also proved amenable for the study of other aspects of population ecology and resulted in a series of papers on the control of fecundity (e.g. Gilbert 1988) and a series of papers on insects and temperature, one of which, Gilbert and Raworth (1996), presents a general theory.

The effect of predation on population dynamics was studied using the pea aphid, *Acyrthosiphon pisum* (Harris) on alfalfa (lucerne) and ladybird beetles, *Coccinella* spp. The resulting Gilbert-Frazer predator-prey model represented a major advance in population ecology, and the work produced one of the first cases in which the population dynamics of an insect in the field were explained by quantitative assessment of predation processes at lower levels (Frazer and Gilbert 1976). A key result was that, contrary to current theory, the population dynamics of the aphid are intrinsically unstable, being determined largely by weather via its effects on predation. Having considerable experience with the system, the group conducted an interesting applied study when Visiting Scientist, Eric Charnov arrived in the mid 1970's. The researchers set up several types of fisheries within an alfalfa field (four different, constant rates, and two increasing rates, of exploitation) - the pea aphid played the part of the fish. Analyses of catches in the various fisheries showed how compensatory mortality within the system can affect catch-versus-effort data and result in overestimation of potential catches based on those data (Charnov *et al.* 1976). Penny Ives joined the group in the late 1970s conducting detailed work on the estimation of coccinellid numbers, beetle movement in the field, and the relationship between feeding rate and egg production. The work culminated in a collection of nine papers covering the complete predator-prey relationship (Baumgärtner *et al.* 1981).

In order to generalize about population processes it was necessary not only to compare studies of different organisms, but also the same organism in different parts of the world. This was done with many of the studies of *P. rapae*. In addition, David Raworth undertook studies of the population dynamics of the cabbage aphid, *Brevicoryne brassicae* (L.) (e.g. Raworth 1984), an aphid that had been intensively studied in Australia by Dick Hughes at CSIRO; and Vince Nealis undertook comparative studies of the ecology of *Cotesia rubecula*, a parasite of *P. rapae*, in Vancouver, BC and Canberra, Australia (Nealis 1985).

What were the circumstances that led to this group? The work arose from the interests and dedication of the people involved. Inspiration came from the three lead researchers: Neil Gilbert, who trained at Cambridge as a biometrician under R.A. Fisher; Andrew Gutierrez who trained in population ecology at UC Berkeley under R. van den Bosch; and Bryan Frazer, who trained in entomology at UC Berkeley under R. van den Bosch. It was Neil Gilbert's unique view of population ecology, his insight that focused on fundamental ecological questions, his rigorous approach in 'consulting the animals and plants', and his drive, that guided much of the work. C.S. (Buzz) Holling (Director of the IARE) recognized the importance of Neil's views and supported him in a research position that required little teaching - although many students will attest to the influence Neil had on their work. The group was influenced by other workers who were making important advances in quantitative population ecology at the time, for example: C.S. Holling had taken a quantitative, reductionist approach to predation processes (Holling 1965); and R.F. Morris produced a series of papers on the quantitative assessment of the population dynamics of fall webworm, *Hyphantria cunea* Drury (e.g. Morris 1971). Advances in computer technology very much facilitated the work. Government-funded summer employment programmes provided the many hands that are necessary to conduct field studies in population ecology. Finally, the research was driven predominantly by scientific considerations – this required a unique economic, and administrative climate.

The work is not finished. Long-term, science-directed studies in quantitative population ecology are still very much needed to gain further insights into the complex relationships and processes that result in the various scale-dependent patterns of insect distribution and abundance.

Population ecology of forest Lepidoptera

The history of forest entomology in British Columbia can be organized around the species of insect under study. In the mid-1950s W.G. Wellington moved to the Pacific Forestry Laboratory and began working on the western tent caterpillar, *Malacosoma pluviale californicum* (Dyar). In his previous work Wellington developed his ideas on the interactions between insects and weather. In BC he was welcomed to an outbreak of tent caterpillars on the Saanich Peninsula of Vancouver Island between 1955-57. Here Wellington monitored changes in both the numbers and frequency of tent types; elongate tents were thought to characterize active groups and compact tents sluggish groups (Wellington 1960, 1964, 1965). He described how simple behavioral tests could distinguish the "quality" of individuals and how the composition of families in terms of how many active or sluggish individuals occurred, could influence their success. He also related this to the impacts of climate, parasitoids, and disease. During the 1970s Wellington and colleagues at the Institute of Animal Resource Ecology at UBC (Ilan Vertinsky and Bill Thompson) explored the potential interactions between heterogeneity in larval quality, climate, and population density of tent caterpillars using simulation models. A recent review of the tent caterpillar work (Myers 2000) looks at which of the early observations have been repeatable in subsequent population cycles. Tent shape does not seem to be a good predictor of population condition, but a common observation is a sudden invasion of new habitat sites associated with peak populations. Work on the viral disease that occurs in peak populations has continued, as has work on the impacts of weather.

Wellington was a strong force in encouraging people to recognize that all individuals in a population are not the same and that those in increasing populations may be quite different from those in declining populations. The actual causes of population decline may be less important than the condition of individuals within the population. These ideas have important ramifications for the simple density-dependence approach to population ecology. In addition he emphasized how geographic variation in weather patterns could have long-term influences on insect populations and distributions. These ideas take on new relevance with the current interest in global climate change.

During the 1970s, outbreaks of both the eastern, *Choristoneura fumiferana* (Clemens), and western spruce budworms, *C. occidentalis* Freeman, attracted the attention of insect ecologists across the continent. C.S. Holling and Don Ludwig (Ludwig, *et al.* 1978) spearheaded modeling efforts to explore the dynamics of these species (McNamee, *et al.* 1981). This involved the development of both very complicated simulation models and very simple deterministic models. At this time there was considerable interest in catastrophe theory and the idea that there could be multiple stable states at low and high densities, with very rapid transitions between. Part of this idea was that insects could be maintained in a low-density "predator pit" until good conditions allowed them to break out and move to a new, high-density equilibrium.

Other work on the western spruce budworm was initiated from the Pacific Forestry Centre by Roy Shepherd. In the mid-1970s a prolonged outbreak of populations in the vicinity of Hope led to calls for a spray program. Like many spray programs this was controversial because the insect ecologists considered the populations to be on the verge of collapse. The newspapers were filled with controversial articles and Shepherd was on the hot seat. Shepherd's group did considerable work on the western spruce budworm including trials with viral sprays and Bt.

Douglas Fir Tussock moth, *Orgyia pseudotsugata* (McDunnough), is another forest defoliator with cyclic population dynamics, and a periodic pest in BC. Imrie Otvos and Shepherd initiated trials with a virus spray that showed that it was possible to stop an outbreak (Shepherd, *et al.* 1984). Viral sprays are still in the toolbox of potential controls for Tussock moth. These trials are excellent examples of applied insect ecology. Shepherd also carried out considerable work on monitoring tussock moth including developing pheromone systems to allow predictions of impending outbreaks.

The introduced winter moth, *Operophtera brumata* (L.), made a mark on insect ecology in BC starting in the late 1960s. By the early1970s what was thought to be an outbreak of the native Bruce's spanworm, *O. bruceata* (Hulst), continued to cause unsightly defoliation of oak trees in Victoria. Finally, studies by Dave Gillespie and Thelma Finlayson (Gillespie *et al.* 1981) on the parasitoids of the caterpillars led to the realization that this was an exotic species and therefore lacking in parasitoids. Winter moth had been successfully controlled in Nova Scotia by the introduction of a parasitoid fly, *Cyzenis albicans* (Fall.) and the experiment was replicated in Victoria. Within 5 years of the original fly introductions winter moth populations declined. Jens Roland did his Ph.D. research on this successful biological control program and showed through his experiments and observations how ground predators and parasitoids interact to maintain winter moth at densities higher than in their native habitat but much lower than during their initial outbreak (Roland 1988, 1994; Roland and Embree 1995). Studies continued when winter moth became a pest of blueberries on the lower mainland (Horgan *et al.* 1999). Imrie Otvos was given the keys to the city by an appreciative Victoria city council for the successful biological control of winter moth.

Gypsy moth, *Lymantria dispar* (L.), has also presented challenges to insect ecologists in BC. This exotic, European species, which is well established in eastern North America continues to show up in BC. The first discovery of the species was in the early 1900s when the Asian strain was found. However, it wasn't until 1978 that a major introduction was recognized in Kitsilano. The challenge of this species to insect ecologists has been to detect introductions and coordinate spray programs. Many introductions have either gone extinct or have been eradicated with *Bt* sprays (Myers and Rothman 1995). Again these spray programs have been controversial and have involved considerable attention of insect ecologists.

One of the fine aspects of population studies of forest insects was the Forest Insect and Disease Surveys that were done annually from the 1930s to the mid-1990s. These data bases provided valuable long-term information on population trends of many of British Columbia's forest caterpillars. That they have stopped just as the world is becoming increasingly interested in the impacts of global change is a shame.

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