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Long-term population dynamics of western tent caterpillars: History, trends and future prospects
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Abstract

1. This is a story of unique long-term studies of the population ecology of a gregarious, tent-building, forest-dwelling caterpillar, the western tent caterpillar (*Malacosoma pluviale* Dyar), and its parasitoid, the Braconid wasp *Meteorus ivensi*, in the Pacific Northwest, USA. Particularly in cyclic populations (hereafter, "outbreaks"), the caterpillar causes defoliation of deciduous trees, which can have consequences for ecosystem processes and services, such as timber production and carbon sequestration. Thus, cyclic outbreaks have prompted considerable attention of extension from population ecologists (Myers, 2018).
2. We whole-population and individual-based long-term studies focused on predators, parasitoids, pathogens and the environment and/or by tertiary factors, such as behaviour and phenology, which influence host-parasitoid interactions (Myers, 1988; Myers & Cory, 2016). Our research has contributed to understanding how host-parasitoid interactions can generate cyclic population dynamics, how host-parasitoid interactions can be affected by climate change (Hazen et al., 1993), interest in overwintering mechanisms and the self-regulation of arthropod population cycles (Myers & Cory, 2016).
3. Heat could variation among individuals play a role in population regulation? Most research on host-parasitoid interactions assumes that individuals are identical (Hassell, 1978). We hypothesize that the consumption of heterogeneous resources by individual caterpillars may influence their susceptibility to parasitoids. We found that the parasitoid *Meteorus ivensi* (Braconidae) preferred heavily feasted caterpillars. Parasitized caterpillars spun fewer silken tents than unparasitized caterpillars, which may reduce parasitoid survival or plant herbivore protection.
4. Our research has implications for forestry management. Our research has implications for management of forest ecosystems. Cyclic defoliation of forests by caterpillars can have consequences for ecosystem processes and services. Forestry practices can influence host-parasitoid interactions, which may influence the ecological effects of tent feeding.
5. Introduction and ongoing experiments were unsuccessful at releasing such of our parasitoids into populations of western tent caterpillars. Future research on the ecology of host-parasitoid interactions and population cycles is needed.
6. Warming temperatures influence the phenology of egg hatch and leaf development in ways that may decouple host-plant phenology from that of the caterpillar (Hazen et al., 2011). Loss of refuges or alternative prey may destabilize host-parasitoid interactions (Hassell, 1978). Climate change may also influence host-parasitoid interactions by affecting the phenology of host-parasitoid interactions and population cycles and influence the theory of cyclic dynamics. The early focus on host-parasitoid interactions and population cycles in insects, including the western tent caterpillar, has contributed to both scientific and applied ecology and forestry.

1 | INTRODUCTION AND HISTORICAL CONTEXT FOR CYCLIC DYNAMICS

Cyclic population dynamics of herbivorous arthropods (Myers & Cory, 2016; Hassell, 1978). Fluctuating or cyclic population dynamics of herbivorous arthropods have been of considerable interest to ecologists and economically important to forestry, agriculture and human health. Thus, cyclic population dynamics have prompted considerable attention of extension from population ecologists (Myers, 2018).

Our whole-population and individual-based long-term studies focused on predators, parasitoids, pathogens and the environment and/or by tertiary factors, such as behaviour and phenology, which influence host-parasitoid interactions (Myers, 1988; Myers & Cory, 2016). Our research has contributed to understanding how host-parasitoid interactions can generate cyclic population dynamics, how host-parasitoid interactions can be affected by climate change (Hazen et al., 1993), interest in overwintering mechanisms and the self-regulation of arthropod population cycles (Myers & Cory, 2016).

How could variation among individuals play a role in population regulation? Most research on host-parasitoid interactions assumes that individuals are identical (Hassell, 1978). We hypothesize that the consumption of heterogeneous resources by individual caterpillars may influence their susceptibility to parasitoids. We found that the parasitoid *Meteorus ivensi* (Braconidae) preferred heavily feasted caterpillars. Parasitized caterpillars spun fewer silken tents than unparasitized caterpillars, which may reduce parasitoid survival or plant herbivore protection.

Our research has implications for management of forest ecosystems. Cyclic defoliation of forests by caterpillars can have consequences for ecosystem processes and services. Forestry practices can influence host-parasitoid interactions, which may influence the ecological effects of tent feeding.

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2 | THE WESTERN TENT CATERPILLAR SYSTEM

The Pacific Northwest, Washington, or inland population ecologists, turned the attention to outbreaks of cyclic western tent caterpillars *Malacosoma californicum pluviale* (Dyar) (Lepidoptera: Lasiocampidae) (Myers, 1988; Myers & Cory, 2016). Outbreaks of this species have caused considerable damage to cultivated fruit and forest trees (Myers, 1988). The interest in variation among individuals's impact on high and low density populations. Population ecologists have long been interested in the self-regulation of arthropod population cycles (Myers, 1988). Population ecologists have long been interested in the self-regulation of arthropod population cycles (Myers, 1988). Population ecologists have long been interested in the self-regulation of arthropod population cycles (Myers, 1988). Population ecologists have long been interested in the self-regulation of arthropod population cycles (Myers, 1988).

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FIGURE 1 Population cycles in western tent caterpillars (WTC) in Lopez Island (WTC1) and Orcas Island (WTC2) in the Washington Archipelago, USA.

(Sarfraz, Kharouba, et al., 2013). To further investigate the influence of warming on egg hatch and budburst, Kharouba et al. (2015) placed aerated plastic bags over branches of red alder trees with deployed egg masses. This increased the local temperature (2.93°C [0.18 SE]) and caused earlier egg hatch, but did not modify leaf development. Larvae from eggs that hatched as much as 25 days before leaf emergence had high survival and were resistant to starvation (Kharouba et al., 2015). These experiments lead us to conclude that the variation in spring conditions from year to year slows directional selection on the mismatch between egg hatch and leaf development and promotes resilience to starvation. Western tent caterpillars appear to be well adapted to variation in spring weather.

10.2 Temperature and virus transmission

Temperature can influence factors related to larval development, disease immunity and activity, all of which could influence virus transmission and survival. The key question is whether warmer temperatures translate to changes in viral dynamics at the population and field level. Laboratory experiments showed that temperature had no effect on the innate susceptibility of larval WTC to the virus (Frid & Myers, 2002). In the field, temperatures in May have only increased by about 1°C over the years we have studied WTC, and the average levels of infection in the populations showed no signal of change at a broad level (MacDonald et al., 2023). This is not surprising given the small change and the strong effect of population density on infection and its high variability over time.

Basic susceptibility is only part of disease transmission. A warming climate is likely to increase activity in ectotherms and in a disease system where the pathogen is primarily acquired horizontally by feeding, transmission and infection should increase through behavioural change. In laboratory studies, feeding activity and larval growth of WTC increased with temperature (MacDonald et al., 2023). Virus-infected larvae also died more rapidly with increasing temperature; this might be expected to reduce the number of transmission stages (OBs) produced, but yield surprisingly remained the same (MacDonald et al., 2023).

Next, we tested how temperature effects on larval feeding and activity might impact virus transmission at the population level. In a greenhouse experiment at two temperatures, one ambient and the other approximately 10°C warmer, virus was introduced to occupied tents by releasing pre-infected larvae and later, 'healthy' larvae were collected to monitor the infection. Contrary to our predictions, virus infection and transmission were greater at the cooler temperature, although larval movement and feeding were greater, as expected, at the higher temperature (MacDonald et al., 2023). Because larvae were less active at cooler temperatures, they spent more time on the tent and more importantly, more insects died on the tents, thus exposing the healthy larvae to the virus. This outcome parallels the suggestion of Wellington and co-workers (Iwao & Wellington, 1970) that viral infection was related to the activity levels of larvae. Sluggish larvae in compact tents were more likely to succumb to disease than more active larvae in elongate tents during the population decline, although this was not related to temperature.

11 SUMMARY AND CONCLUSIONS

This unique, prolonged study of tent caterpillars identifies the consistent changes in fecundity, early larval survival and viral infection over time and with population density. The contributors to population decline are reduced fecundity and viral infection in peak populations. A key issue is what causes the reduction in fecundity? Sublethal effects, food limitation and reduced leaf quantity and quality are all possibilities. The similar patterns of increase and decline in fecundity and early larval survival indicate that conditions may change with increasing density before infection levels become high. Continued poor larval survival and reduced fecundity during the decline phase provide the delayed density-dependent factors to create cyclic dynamics.

Over this study we used many field and laboratory experiments to test hypotheses about the relationships between insects, host trees and viral infection (Table 1). A remaining question is why populations with different histories, either experimental introductions or natural dispersal, decline in synchrony. Although some experiments show influences of larval feeding on leaf quality reflected in moth size or fecundity, these simultaneous population declines do not reflect a history of feeding on host trees.

TABLE 1. Hypotheses about interactions of western tent caterpillar (WTC) with host plants, temperature and viral infection tested over the years of study.

Hypotheses tested	Result	Citations
Individual variation in larval activity and tent shape changes with density	No	Myers (1990)
Cropping a population to prevent outbreak and foliage quality reduction delays outbreak	No	Myers (1981)
Introductions to new areas will delay population peak and decline	No	Wellington (1960) and Myers (1990)
Moths spread from areas of initial outbreak	Yes	Wellington (1957, 1960) and Myers (1990); Figures 3 and 5
Populations will vary genetically between areas and peaks	No	Franklin et al. (2014)
Fecundity and tent size change with population density	Yes	Myers (2000, 2018) and Myers and Cory (2013); Figure 3
Fecundity is related to population growth	Yes	MacDonald (2016); Figure 4
Infection by McpiNPV changes with host density	Yes	MacDonald (2016); Figure 4
Infection by McpiNPV is related to population growth	Yes	MacDonald (2016); Figure 4

The study of WTC population dynamics informs the broader field of population ecology and sheds light on the mechanisms behind population cycling and the role of disease in driving these cycles (Myers, 2018). Population cycles are more than just increases and declines in numbers, but a complex pattern of changing characteristics and conditions that must be identified, tested and explained for an in-depth understanding (Barraquand et al., 2017).

12 ECO-EVO DYNAMICS OR PHENOTYPIC PLASTICITY: WHICH IS MORE IMPORTANT?

A major feature of the WTC story is the recognition of phenotypic variability related to population dynamics (Wellington, 1960). Simultaneous with this work came the idea that population density could select the different types of individuals as population density changes and influence population dynamics (Chitty, 1960, 1967). We can ask how these ideas fared with time. For Wellington, most of the variation he proposed did not change with population density (Supporting Information S1), except for fecundity. Chitty's hypothesis of genetic change, although widely investigated, has never been supported for cyclic mammal populations for which it was developed. Even so, it is often cited in the eco-evo literature (Bassar et al., 2021; Govaert et al., 2019; Reznick et al., 2019).

Our work and Wellington's show repeatable changes in fecundity over the population cycle from high in the increase phase to lower during the peak and decline. This is most likely a phenotypically plastic feature that is influenced by food plant quality and quantity, and possibly sublethal infection. In addition, variation among families in resistance to NPV is very high, and if this has a genetic basis, it could be selected on (Cory & Myers, 2009). Resistance was higher following the epizootic at peak density, suggesting selection occurred. The relevant factors in this system are an increase in population numbers and associated increase in levels of viral infection (ecological factors) with possible selection for greater resistance over the viral epizootic (evolution). Thus, selection possibly acts on the ecological time scale (Bassar et al., 2021).

A similar situation has been described in another cyclic Lepidoptera, the spongy moth, *Lymantria dispar*. Dwyer et al. (2022) developed a population model that included a shift in resistance to viral infection over the epizootic. They included a cost of resistance associated with fecundity based on earlier work (Elderd et al., 2008; Páez et al., 2017), that also showed heritability of resistance which we did not find in WTC. Elderd et al. found reduced infection in three out of five populations post infection indicating that selection can occur. The Dwyer et al. (2022) model indicates more realistic dynamics after adding variation in resistance, and they propose that this fits the eco-evo paradigm, one of few examples based on field data.

We suggest that the importance of phenotypic variation in physiology, behaviour and morphology (fecundity) created through stress, food limitation, responses to predators etc., may be overshadowed by the interest in eco-evo dynamics. Phenotypic plasticity (Stearns, 1989) can explain the rapid change in fecundity and influence the cyclic population dynamics of populations. Although much of the variation among individuals proposed by Wellington to be relevant to population dynamics did not show consistent patterns (Supporting Information S1), changing fecundity and viral infection have proven to be important drivers of the cyclic dynamics of WTC, and phenotypic variation in reproduction is likely to be relevant in the dynamics of other cyclic species (Myers, 2018).

AUTHOR CONTRIBUTIONS

This paper is a retrospective of 70 years of studies of the western tent caterpillar in British Columbia. Studies by Judith H. Myers were started in the 1970s and studies of NPV were guided by Jenny S. Cory from 1990 onward. The manuscript was initially prepared by Myers and developed through discussion and detailed editing by Cory. This work has been a collaborative effort by us and our students at the University of British Columbia and Simon Fraser University.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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