

Effects of phenological synchronization on caterpillar early-instar survival under a changing climate¹

Emma Despland

Abstract: Early-instar caterpillars experience very high and often very variable mortality; if it is density dependent, it can be a key factor in outbreak dynamics. Plant physical and chemical defenses can be extremely effective against young caterpillars, even of specialists. Phenological asynchrony with host plants can lead to dispersal and mortality in the early instars and increased predation or poor nutrition in later instars. Predation on early-instar larvae (including cannibalism) can be extremely high, parasitism appears generally low, and pathogens acquired early in larval development can lead to high mortality in later stadia. Four well-studied species reveal very different roles of early-instar mortality in population dynamics. In spruce budworm and gypsy moth, early-instar mortality rates can be very high; they do not drive outbreak cycles because density dependence is weak, but can modulate cycles and contribute to outbreak size and duration. For the autumnal moth, early-instar survival depends on host plant synchrony, but may or may not be density dependent. For monarch butterflies, the relative importance of larval mortality rates in population dynamics remains unclear. Tritrophic interactions between herbivores, host plants, natural enemies, and microbes play complex and species-specific roles in early-instar ecology, leading to emergent dynamics in population fluctuations. The phenology of these relationships is often poorly understood, making their responses to climate change unpredictable.

Key words: Lepidoptera, hatchlings, synchronization, outbreaks.

Résumé : Les chenilles des premiers stades larvaires connaissent des taux de mortalité très élevés et souvent très variables; si ces taux varient avec la densité, ils peuvent devenir un facteur clé dans la dynamique des épidémies. Les défenses physiques et chimiques des plantes sont souvent extrêmement efficaces contre les jeunes chenilles, même celles des espèces spécialisées. L'asynchronie phénologique avec les plantes hôtes peut entraîner la dispersion et la mortalité chez les premiers stades larvaires, et une augmentation de la prédation ou une mauvaise nutrition chez les derniers stades larvaires. La prédation lors des premiers stades larvaires (incluant le cannibalisme) peut être extrêmement élevée, le parasitisme semble généralement faible et les pathogènes qui infectent tôt dans le développement des larves peuvent entraîner un taux de mortalité élevé chez les stades ultérieurs. Quatre espèces bien étudiées révèlent différents rôles de la mortalité chez les premiers stades larvaires dans la dynamique des populations. Chez la tordeuse des bourgeons de l'épinette et la spongieuse, les taux de mortalité peuvent être très élevés chez les premiers stades larvaires; ils n'ont pas d'effet déterminant sur les cycles épidémiques parce que la dépendance à la densité est faible, mais ils peuvent moduler les cycles et contribuer à l'ampleur et à la durée des épidémies. Dans le cas de l'épirrite automnale, la survie des premiers stades larvaires dépend de la synchronie avec la plante hôte, mais peut ou non dépendre de la densité. Dans le cas du monarque, l'importance relative du taux de mortalité des larves dans la dynamique des populations demeure incertaine. Les interactions tritrophiques entre les herbivores, les plantes hôtes, les ennemis naturels et les microbes jouent des rôles complexes et propres à chaque espèce dans l'écologie des premiers stades larvaires qui mènent à des dynamiques émergentes dans la fluctuation des populations. La phénologie de ces relations est souvent mal comprise, ce qui rend leurs réponses au changement climatique imprévisibles. [Traduit par la Rédaction]

Mots-clés : lépidoptères, larves, synchronisation, épidémies.

Introduction

"...plague and predation are part of the warp and woof of nature.... The tent caterpillars are no exception.... The colony that had welcomed spring 200 hundred strong had been reduced to half its number. The enormous population of tent caterpillars had been cropped by weather, starvation, ants, bugs, parasites, fungi, viruses, bacteria, and misadventure in general. It had been a particularly trying year. Summer had hardly begun and the die had already been cast for the year

to come. There would be fewer moths, fewer egg masses, and fewer colonies in the next generation. As with all species, not excluding mankind, the reproductive potential, the birth rate, genetically built in, generated an inexorable tide. Only the competing tides of multitudinous species all striving for their share of the finite materials of the planet keep the flood of life at an even level. The flood was never placid, and the waves, sometimes ripples, sometimes huge swells, reflected the fierce underlying competitive struggles. The

Received 22 December 2016. Accepted 12 March 2017.

E. Despland. Biology Department, Concordia University, 7141 Sherbrooke St. West, Montreal QC H4B 1R6, Canada.

Email for correspondence: Emma.Despland@concordia.ca.

¹This paper is one of a selection of papers from the IUFRO workshop "Effect of climate change on boreal pest range shifts and their ecological consequences", hosted by the IUFRO Boreal and Alpine Forest Ecosystem Unit Working Group 8.01.06 and co-sponsored by working groups 7.03.07 (Population Dynamics of Forest Insects) and 7.03.05 (Ecology and Management of Bark and Wood Boring Insects), held in Sept-Îles and Baie Comeau, Quebec, on 11–15 July 2016.

Copyright remains with the author(s) or their institution(s). Permission for reuse (free in most cases) can be obtained from [RightsLink](https://www.elsevier.com/locate/permissions).

rise and fall of the tent caterpillar populations from one year to the next, from one phase of a cycle to another, was just one facet mirroring the perpetual competition.” (Dethier 1980)

Most Lepidoptera are r-selected, meaning that populations are governed by maximum reproductive capacity. Large numbers of eggs are laid in each generation, but survival rate is low. The high number of fragile offspring means that population growth rate can vary tremendously with survival rate of those offspring, generating dramatic fluctuations in population size. Phenology mediates the interactions between herbivores, host plants, and natural enemies and can therefore play a key role in determining survival rates. A changing climate can perturb these phenological relationships, with potentially dramatic consequences for population sizes (Parmesan 2006; van Asch and Visser 2007; Boggs 2016). The current paper will explore the vulnerability of neonate larvae to these phenological mismatches and its role in population dynamics under climate change.

Early-instar biology

Neonate caterpillars face several considerable challenges upon hatching: they need to overcome plant mechanical (e.g., spines, trichomes, surface waxes, tough cuticles) and chemical defenses (including secretions) and initiate feeding, before exhausting the resources with which their mothers provisioned their eggs, and without being dislodged from the plant by wind and rain or falling prey to natural enemies.

Early-instar caterpillars are not merely smaller versions of their final-instar selves; they not only differ in scaling properties (e.g., mandible size and strength, thermal mass, surface to volume ratio) but also in metabolism, digestive physiology, sensory modalities (Hochuli 2001), and gut microbiota (Mason and Raffa 2014). In general, young caterpillars have higher relative growth rates, consumption rates, metabolic rates, and assimilation efficiency, but lower net growth efficiency, than older ones (Scriber and Slansky 1981; Johnson and Zalucki 2007). They are more selective of food sources and more sensitive to plant chemistry, possibly due to a more limited array of digestive enzymes (Hochuli 2001). They are hence often more vulnerable to plant compounds and pathogens that have little effect on older individuals (Zalucki et al. 2002). These small larvae usually have limited vision, but are often positively phototactic and negatively geotactic, and also respond to olfactory and gustatory cues (Perkins et al. 2008). Many species start out cryptic, acquiring warning coloration later in development, and many others are gregarious in the early instars, becoming solitary as selection pressures change with increasing size (Despland 2013).

Mortality rates of early instars

In the normal course of events, r-selection implies that most individuals die. Indeed, studies on lepidopteran population dynamics show that the early instars experience huge attrition (Zalucki et al. 2002), such that type III survivorship curves (with most mortality occurring in the early stages) are the most common in lepidopteran life histories (Floater and Zalucki 1999).

For instance, among forest defoliators, one study shows forest tent caterpillars, *Malacosoma disstria*, to experience 61%–66% mortality in the first three larval instars in aspen and mixedwood stands in Alberta, Canada (Nixon and Roland 2012). At the other end of the world, on acacias in Queensland, Australia, the gregarious processionary caterpillar *Ochrogaster lunifer* experienced over 50% mortality in the first larval stage across all populations studied, with 82% of colonies wiped out before the end of larval development (Floater and Zalucki 1999). In both cases, the most important cause of early-instar mortality was arthropod predation.

Among agricultural pests, a *Pieris rapae* life table shows 61% mortality during the first instar mostly due to predation and drowning, with parasitoids gaining in importance later in larval

development (Dempster 1967). Codling moth, *Cydia pomonella*, first-instar larvae on pear suffered 55% mortality in the first larval instar, linked to lignification preventing larval entry to the fruit (Westigard et al. 1976).

Nonpest butterflies have received less attention, but appear to suffer similar high attrition rates: in the first 2 days post-hatch, *Heliconius* caterpillars feeding on neotropical *Passiflora* vines experienced 70% mortality on plants without ants attending extrafloral nectaries, but 45% on ant-attended plants (Smiley 1985). The sulphur butterfly *Colias alexandra* in montane valleys in the Rockies suffered between 37% and 52% mortality in the first instar and between 32% and 60% in the second, averaging 90% in the first three pre-diapause instars, attributed mainly to failure to establish feeding or dislodgment from the host plant (Hayes 1981).

A review by Zalucki et al. (2002) shows that mortality in the early instars is often not only very high but also extremely variable. Notably, it does not identify any clear patterns with life history traits: there is no obvious difference between concealed and open feeders, batch or solitary laid eggs, specialist versus polyphagous feeders. Variance is often so high, even within species, between years, sites, or host plants that it is difficult to generalize about the adaptive value of different traits (Zalucki et al. 2002). This high variability also implies volatile population dynamics, where endemic populations, undetectable in the early instars, can cause heavy defoliation only weeks later if unusually large numbers survive to the later instars.

Population processes clearly depend on survival at all life stages. Successful management or conservation requires identifying key stage(s) influencing population dynamics. Life history stages with density-dependent mortality will be important in regulating population size: if density dependence is direct (mortality increases with increasing population size), it will tend to stabilize populations, but lagged (i.e., higher order) density-dependent mortality tends to increase population fluctuations and even generate outbreaks (Cooke et al. 2007). Understanding rates and causes of mortality at all life history stages thus has practical implications for managing population dynamics.

Sources of early-instar mortality

The small size of first-instar caterpillars implies that they can be dislodged from the host plant by a falling raindrop (personal observation). Most life table studies include a substantial category labelled “unknown” or “disappeared”, which likely reflects the high frequency of such accidents.

Failure to establish on plants is often cited as a cause of early-instar mortality; the explanatory value of this observation is limited, but it is likely linked to plant defensive traits. Spines and trichomes can prevent small larvae from accessing the leaf surface (Rathcke and Poole 1975), toughness can prevent small mandibles from piercing the cuticle (Clissold et al. 2009), and secretions can mire and drown neonates (Zalucki et al. 2001b). For instance, leaf area consumption of Siberian elm clones by neonate *Paleacrita vernata* was negatively related to the trichome density (Dix et al. 1996). Plant chemical defenses can decrease food consumption, decrease growth rate, or cause catalepsy or simply death (Scriber and Slansky 1981).

Predation and parasitism have often been thought to be more important in later larval instars (Hawkins et al. 1997), but it is increasingly recognized that mortality of young larvae is often underestimated because they are so small and difficult to study. Indeed, an increasing body of research suggests that predation rates on early-instar larvae can be very high (Zalucki et al. 2002; Nixon and Roland 2012). Cannibalism, of eggs by neonates and of neonates by older larvae, can be an important source both of mortality and of nutrition and is influenced by environmental factors including population density, food nutritional quality (in particular protein content), and synchrony with the host plant

(Richardson et al. 2010). Parasitism appears to be generally low for young instars, but it can be very high on eggs, and since mortality due to parasites is usually delayed, it can be difficult to establish which stage was attacked.

Finally, increasing numbers of studies highlight the effects of microbes (as pathogens or symbionts) on insect performance. For instance, leaf surface microflora can affect herbivores and the scant evidence that exists suggests that pathogens from the phylloplane are more harmful for young than for older caterpillars (Leong et al. 1997). However, the population-level consequences of these interactions remain unresolved.

Phenological relationships under a changing climate

The importance of phenological synchrony between a herbivore's feeding stages and the availability of high-quality plant tissue has long been recognized (Feeny 1970) and has received renewed interest in this era of changing climate (Parmesan 2006; Boggs 2016). Indeed, the timing between insect feeding stages and the deployment of plant defences can be critical for insect survival and development (van Asch and Visser 2007); notably, many insects rely on young expanding foliage, which is generally less tough and more nutritious and hence provides a window of opportunity for insect herbivores (e.g., temperate zone hardwoods (Feeny 1970; Hunter and Elkinton 2000), boreal conifers (Lawrence et al. 1997), and tropical shade-tolerant angiosperms (Kursar and Coley 2003)). These phenological mismatches mostly affect fragile young larvae.

For instance, 69% of *Rhopobota naevana* neonates die before feeding when presented with only old cranberry leaves compared to 11% on young expanding foliage. Population growth is thus five times higher if larvae hatch in synchrony with host bud burst (Cockfield and Mahr 1993). First-instar *Zeiraphera canadensis* show dramatically lower survivorship (from 50%–70% to less than 25%) when fed on 4–5 day old white spruce (*Picea glauca* (Moench) Voss) foliage; in the field, these larvae move in the tree, tracking changes in foliar quality following bud burst away from the most vigorous apical shoots to those with more immature foliage (Carroll and Quiring 1994).

Synchrony with host plant has been suggested as an important factor in the dynamics of many forest pests (see review by van Asch and Visser (2007)). The role of host synchrony can be difficult to ascertain, as many larvae can disperse away from poorly synchronized hosts to phenologically suitable ones if they are available within a reasonable distance (e.g., *Malacosoma disstria* (Donaldson and Lindroth 2008)). This implies that the window of opportunity defined by host phenology is spatial as well as temporal, and consideration of distribution of host phenologies across the landscape is essential to understanding their role in defoliator population dynamics (Foster et al. 2013).

Past debates on the strength of terrestrial trophic cascades, or the relative importance of top-down and bottom-up effects in regulating defoliator dynamics (Schmitz et al. 2004), are increasingly recognized as sterile because host plant traits, natural enemies, microbes, and environmental factors often interact in ways that are complex and species specific, generating unpredictable emergent dynamics that can play a key role in outbreaks (Cooke et al. 2007; Stam et al. 2014). These tritrophic interactions can lead, for instance, to the slow-growth, high-mortality scenario whereby slow development on poor-quality (or poorly synchronized) host plants leads to higher predation in later instars, as caterpillars fail to grow large enough to escape attack before the natural enemies become abundant (e.g., *Malacosoma disstria* (Parry et al. 1998)). This complexity implies that the natural history of individual study systems must be taken into consideration to understand how phenology mediates multitrophic interactions and their consequences for early-instar survivorship. These relationships are explored through four different case studies, chosen for their

differences in natural history, phenological relationships, population dynamics, and responses to climate change.

Early-instar mortality and population dynamics: four case studies

Spruce budworm

The spruce budworm (*Choristoneura fumiferana*) is the most important defoliator of conifers in the Canadian boreal forest. The last major outbreak peaked in the 1970s and damaged or killed trees across nearly 58 million ha, resulting in the loss of about 500 million m³ of timber and costing some \$12.5 billion in Quebec alone in lost revenue in remote areas with few other industries. On Cape Breton Island (Nova Scotia), 71% of merchantable timber was destroyed. A new outbreak is currently underway on Quebec's North Shore and spreading in Gaspésie (Sonntag 2016).

The main regulator of budworm outbreaks is thought to be parasitism on late-instar larvae. An approximately 40 year intrinsic oscillation in population density is generated by lagged density-dependent changes in survival of late larvae and pupae, most likely caused by natural enemies (Royama 1984). This oscillation is well documented, but is imperfectly periodic due to modulation by other secondary factors (Cooke et al. 2007), including variation in early-instar survival (Royama 1984; Régnière and Nealis 2008; Bouchard and Auger 2014).

First-instar spruce budworm larvae hatch from the egg in late summer and, without feeding, molt to the second instar and move to a sheltered spot to build a hibernaculum in which to overwinter. In the spring, budworm that emerge before host budbreak mine old needles (Blais 1952; Trier and Mattson 1997). Recent work suggests that these old needles are difficult to pierce but provide a nutritious food source to those caterpillars that succeed (Fuentealba Morales et al. 2017). When budbreak occurs, larvae move to the bud and complete their development on the high-nutrient expanding foliage. High-quality foliage during bud elongation thus defines a window of opportunity for the budworm (Lawrence et al. 1997).

Early-instar spruce budworm larvae experience extreme variation in mortality rates: for example, survival rate from the first to the third instar declined over the course of an outbreak from 73% (1984) to 4% (1996) at one study site (Régnière and Nealis 2007). Stand-scale life tables have suggested that early-instar survival is linked to variance in the timing of emergence from diapause relative to host budbreak, to the duration of the needle mining period prior to budbreak, to prior defoliation, and to infection with microsporidian parasites (Régnière and Nealis 2008).

One key piece of the puzzle is early spring dispersal by ballooning of second-instar larvae emerging from diapause. Ballooning, or drifting in the wind suspended on a fine silk thread, is very risky and associated mortality is thought to be very high (Johns and Eveleigh 2013), but is almost impossible to measure in a forest setting.

Dispersal and associated mortality depend on bud availability to emerging larvae and therefore are thought to increase with phenological mismatch. In this context, variation in the timing of emergence from diapause can be interpreted as a bet-hedging strategy to ensure that at least some progeny are adequately synchronized with the host plant (Régnière and Nealis 2008). Spring temperature can thus impact early-instar survival via effects on phenological synchrony with the host plant, and landscape-scale analysis of an outbreak showed a significant role for spring temperatures in predicting population growth (Bouchard and Auger 2014). This weather effect is independent of population density; however, it can play an important role in the spatial distribution of outbreaks. Indeed, the northern distribution of the current outbreak is thought to be linked to improved survival on black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.), a more

northern host plant, due to phenological advances in budbreak linked to climate warming (Pureswaran et al. 2015).

Bud availability (and hence early-instar survival) also decreases with prior defoliation, as severely damaged trees produce fewer buds the following season (Blais 1952; Régnière and Nealis 2008; Johns and Eveleigh 2013). This bottom-up effect of defoliation on early-instar survival is a lagged, density-dependent process and therefore can have a significant influence on the duration and severity of outbreaks (Cooke et al. 2007).

Finally, although viral and bacterial epizootics are not thought to significantly affect budworm population dynamics, infection with *Nosema* (a microsporidian parasite) is common in outbreak populations. *Nosema* is generally sublethal and vertically transmitted through the egg. Maternal infection leads to lower overwinter survival, later emergence, later dispersal, and lower success in establishing a feeding site in young larvae (van Frankenhuyzen et al. 2007).

In general, natural enemies seem to play only a minor role in early-instar budworm survival, and the factors that large-scale studies isolate as the strongest predictors are spring weather and prior defoliation (Régnière and Nealis 2008; Bouchard and Auger 2014).

Gypsy moth

European gypsy moth (*Lymantria dispar*) was introduced into eastern North America in 1869 and has since spread across most of the eastern deciduous forest, fluctuating to outbreak densities approximately every 6–10 years. Gypsy moth is a generalist early-spring feeder that can survive and reproduce on hundreds of deciduous and some coniferous hosts (Elkinton and Liebhold 1990).

Mortality of first-instar gypsy moth caterpillars has been estimated between 0% and 84% (Elkinton and Liebhold 1990) and between 0% and 90% (Hunter 1993) on different hosts. Extensive research on gypsy moth population dynamics has shown that density-dependent mortality in late larval stages contributes to gypsy moth fluctuations; this mortality appears mostly due to mammalian predators, nuclear polyhedrosis virus at high population density (Elkinton and Liebhold 1990), and, since 1989, a fungal pathogen (Hunter and Elkinton 2000).

However, Elkinton and Liebhold (1990) also stated that “changes in factors that affect survival of early instars may in certain years result in densities of late instar larvae or pupae that approach the satiation points of predators” and hence contribute to outbreak dynamics. One major source of variation in gypsy moth early-instar survival is the extent and success rate of first-instar dispersal by passive ballooning. Adult female moths are flightless and lay their eggs close to their pupation site, often on tree trunks. Field studies indicate that almost all first-instar larvae undergo an initial dispersal episode to settle on host foliage, and some can balloon several times if they do not encounter suitable food. Most first-instar larvae move only a few hundred metres, while some can cover up to a few kilometres (Capinera and Barbosa 1976). Field experiments in which larvae were released near small trees showed that less than 10% reached the foliage, suggesting that dispersal mortality is very high (Capinera and Barbosa 1976) and prompting further research into conditions under which larvae disperse, since these can play an important role in population dynamics.

First instar gypsy moth are susceptible to starvation if they cannot find suitable host leaves within 5–10 days depending on temperature (Hunter 1993) and are more likely to disperse when they only encounter unacceptable food or are denied food (Capinera and Barbosa 1976). Further studies showed that neonates are more likely to disperse from poor-quality (Elkinton and Liebhold 1990) or phenologically unsynchronized hosts (Erelli and Elkinton 2000; Hunter and Elkinton 2000), and when weather is poor during this dispersal phase, the associated mortality increases (Hunter 1993). The window of opportunity for

early-instar feeding is thus linked to dispersal abilities and can be defined in both temporal and spatial terms (Hunter and Elkinton 2000). Indeed, thanks to its polyphagy, a neonate gypsy moth larva on a tree that has not yet leafed-out is often able to disperse to a different species that has. However, phenological mismatch (leaf-out too early or too late) often occurs over large enough spatial scales such that dispersing larvae cannot find suitable food. Foster et al. (2013) showed this occurred in 5 of 11 years studied. Their study also showed that, in an average year, 60% of their Appalachian landscape included host trees with suitable phenology for the gypsy moth but that these stands occurred in different parts of the landscape in different years and were often too far apart for larvae to disperse between them. Early-instar dispersal mortality thus depends on tree species and stand mix but also on spatial heterogeneity in tree phenology (Foster et al. 2013). Finally, larvae that hatch late relative to host plant phenology appear to experience lower predation rates later in larval development such that phenological synchrony and dispersal early in development play a role in population fluctuations via effects on late-instar mortality (Hunter and Elkinton 2000).

Similarly, pathogen-induced mortality in the late larval instars varies according to the species and phenology of foliage ingested with the virus, and this effect is correlated with levels of hydrolysable tannin, suggesting a trade-off whereby plant defenses both hinder insect growth and protect the insect from disease (Cory and Hoover 2006). Recent work shows that late-emerging insects that are limited to feeding on mature foliage (which contains higher tannin levels) are more susceptible to nuclear polyhedrosis virus (Martemyanov et al. 2015) but less susceptible to *Bacillus thuringiensis* infection (Martemyanov et al. 2016). The underlying mechanisms are not understood but could be related to effects on midgut biota: late-emerging larvae show dramatic decreases in the diversity of the midgut bacterial community (Martemyanov et al. 2016). The relationship between pathogens and foliar chemistry, notably phenology and induced defenses following defoliation, in their effects on gypsy moth outbreak dynamics remains difficult to establish (Cory and Hoover 2006).

Finally, it has been suggested that maternal effects increase dispersal rates of gypsy moth neonates (Rossiter 1991) as an adaptive response to decreasing stand quality following several years of defoliation during an outbreak. Dispersal occurs before feeding and therefore depends on the resources in the egg acquired by the mother during her own larval stage (Diss et al. 1996). Leonard (1970a, 1970b) found that smaller eggs from dense populations produce larvae with a longer pre-feeding period and a higher activity level, even in the presence of suitable food, and suggested that these larvae have a greater tendency to disperse. However, more recent work has failed to replicate this result (Diss et al. 1996) and suggests that the most important factors in dispersal-associated mortality are host-plant synchrony and weather during dispersal, not maternal quality or population density (Erelli and Elkinton 2000).

The last significant gypsy moth outbreak in North America occurred in 1981. In 1989, a population upsurge was checked by an accidentally introduced Asian fungal pathogen, aided by high rainfall in May and June of that year (Hajek et al. 1990). Outbreaks essentially ceased until 2015 when drought conditions in May and June prevented the fungus from controlling an upsurge that expanded into high defoliation rates in 2016 (University of Massachusetts Center for Agriculture, Food and the Environment). Whether this represents a climate-change-induced regime shift remains to be seen.

Autumnal moth

The autumnal moth (*Epirrita autumnata*) is a European generalist univoltine geometrid moth; destructive outbreaks occur with a 10 year cycle in northern and high-altitude populations of moun-

tain birch (*Betula pubescens* ssp. *czerepanovii* N. I. Orlova), whereas southern populations are more stable. This suggests that mortality sources are lagged density dependent in the north but directly density dependent in the south (Ruohomäki et al. 2000). Despite considerable research, it is still not clear which mortality agents are responsible for these different dynamics, but the two main factors identified to potentially have density-dependent effects are natural enemies and plant defenses (Ruohomäki et al. 2000).

Natural enemies can cause very high mortality rates, up to 100% at some sites (Tanhuanpää et al. 2001; Klemola et al. 2014). All larval stages are parasitized, but not necessarily by the same species (Kaitaniemi and Ruohomäki 1999). A recent study showed that parasitism rates are highest in the egg and pupal stages but also suggested that mortality in different populations and outbreak cycles can be dominated by not only different parasitoid species but also by different different guilds (egg versus larval versus pupal parasitoids) (Klemola et al. 2014). In general, larval parasitism shows strong lagged density dependence and predicts subsequent population growth rate (Tanhuanpää et al. 2001; Klemola et al. 2014).

Although natural enemy mortality is thought to be highest on late-instar larvae and pupae (Tanhuanpää et al. 2001; Klemola et al. 2014), plant traits clearly affect young larvae. In northern outbreaking populations, autumnal moth larvae hatch at the time of bud burst and feed on the immature foliage of mountain birch (Ayres and MacLean 1987). The larvae can balloon on silk threads but do not disperse far, and dispersal loss is minimal (Tanhuanpää et al. 2001). Birch phytochemistry changes dramatically during leaf elongation (Riipi et al. 2002): flushing leaves contain high levels of flavonoid aglycones internally and on the leaf surface (Lahtinen et al. 2004). As leaves mature, they become tougher and water and nitrogen content decrease, while hydrolysable tannins, flavonoid glycosides, and later proanthocyanidins (condensed tannins) increase (Haukioja 2003). These changes delineate a complex window of opportunity for developing autumnal moth larvae.

At budbreak, the surface of birch leaves is covered with glandular trichomes that secrete exudates containing flavonoid aglycones, which become diluted rapidly as leaves grow. The amounts vary considerably between individual trees but can reach up to 4% of initial leaf mass (Haukioja 2003). Mortality of first-instar larvae is strongly correlated with these compounds and can reach 100% on hosts with high levels of surface flavonoid aglycones in expanding leaves (Lahtinen et al. 2004). However, neonate larvae can at least partially glycosylate these aglycones, rendering them more water soluble and easier to excrete (Lahtinen et al. 2006). Autumnal moth neonates thus possess physiological detoxification mechanisms that suggest an adaptation to feeding on young birch foliage, despite the apparent high mortality. Flavonoids are a complex group of compounds and the efficacy of first-instar detoxification probably varies between compounds (Lahtinen et al. 2006). The amount and chemical structure of flavonoid defenses in flushing leaves could thus be an important predictor of larval survival.

Mature leaves not only contain high levels of condensed tannins (up to 15% of leaf dry mass), they are also very nutrient poor such that later-instar autumnal moth caterpillars need to consume very large amounts to acquire sufficient nutrients. The ratio of leaf consumption to larval growth increases from 2.9 in June to 9.8 in early July and to 15 in August (Haukioja 2003). It appears that young larvae are not able to achieve this rate of consumption on tough foliage or to process these high levels of condensed tannins. Indeed, early-instar larvae grow faster on early-season leaves (Ayres and MacLean 1987). Synchrony of larval hatching and leaf burst is essential for autumnal moth larvae, as early hatching neonates can starve in the absence of open buds and late hatching seldom reach pupation due to delayed development on poor-

quality foliage and high parasitism later in the summer (Ruohomäki et al. 2000).

Rapid-induced resistance (chemical changes occurring in the same season as defoliation, i.e., direct density dependence), delayed-induced resistance (defensive compounds that are produced in the year following heavy defoliation, i.e., indirect density dependence), and indirect defences have long been hypothesized to play an important role in generating autumnal moth outbreaks (Haukioja 2005). Notably, birch defensive compounds can influence both insect growth and immunocompetence, with potentially complex tritrophic feedback involving pathogens (Kapari et al. 2006). Recent molecular studies have proposed mechanisms that could explain rapid-induced resistance (Ruuholta et al. 2008) and delayed-induced resistance (Ossipov et al. 2014) and indirect defense via attracting parasitoids (Klemola et al. 2012) and upregulating defences in neighboring plants (Girón-Calva et al. 2014). However, the importance of these mechanisms in regulating field populations has been very difficult to demonstrate empirically, probably in large part due to considerable interindividual variation and rapid phenological changes in mountain birch phytochemistry (Ruohomäki et al. 2000). Although the ecological relevance of these processes has yet to be determined, they nonetheless raise intriguing questions about the role of early-instar feeding in triggering plant defences and increasing mortality in later stages or later generations.

The *Epirrita* distribution range is expanding into colder, more continental climates, creating novel disturbance regimes in these fragile subarctic ecosystems. Changes in the temporal and spatial scales of *Epirrita* outbreaks, combined with a concomitant range expansion of *Operophtera brumata* into areas previously only affected by *Epirrita*, is changing the dynamics of these mountain birch ecosystems in ways that are not yet clear. Research priorities formulated to address these challenges include a better understanding of thermal and other mechanisms controlling *Epirrita* egg hatch and birch budbreak to predict phenological relationships (Ammunét et al. 2015).

Monarch butterfly

The monarch butterfly (*Danaus plexippus*) is an icon for conservation biology. Monarchs are best known for their extraordinary fall migration from across North America to the mountains of Mexico where they overwinter in reproductive diapause. In early spring, butterflies mate and fly north to the southern United States to lay eggs on emerging milkweeds and die. The next generation migrates farther north, as does the next, until after three or four generations, it is fall again and unmated butterflies emerging in Canada begin the return migration. However, the geographic distribution of *D. plexippus* is much broader: a separate population west of the Rocky Mountains overwinters in California, and nonmigratory populations are found throughout Central America, South America, and the Caribbean as well as more recently established populations in Oceania, Australia, Europe, and Africa (Zhan et al. 2014).

Monarchs are specialists on milkweeds, plants in the genus *Asclepias*, and feed on at least 27 *Asclepias* species of the 100+ found in North America. Early-instar monarch larvae have variable but generally poor survival; average survival rates of first instars vary between 3% and 40% depending on the host plant species (Zalucki et al. 2012). Three traits, latex, cardenolides, and trichomes, have been strongly implicated in milkweed resistance. These traits vary between species and decrease in shade-grown plants (Agrawal et al. 2012). When a milkweed leaf is cut, white viscous latex flows out and hardens upon contact with air. This latex contains cardenolides, steroids that target ATPase regulation and are toxic to animals. Production of cardenolides can also be induced following leaf damage. In some species, glandular trichomes offer an additional mechanical defense and secrete toxic or sticky exudates. Each of these traits has been demonstrated to quantitatively affect

the behavior, performance, and survival of early-instar monarch larvae in the field, despite the fact that these caterpillars are milkweed specialists and have adaptations to cope with them (Zalucki et al. 2012).

Indeed, first-instar monarch larvae exhibit specialized foraging behavior: once they have hatched from their egg and eaten part or all of the egg shell, they closely graze down trichomes to reach the surface and then carefully chew trenches through the epidermis to create a latex-free feeding zone (Agrawal 2012). Nonetheless, neonates can become mired in latex and permanently stuck when it hardens. Ingestion of latex can also cause larvae to become cataleptic and increase their chances of being mired, falling off the plant, or being killed by invertebrate predators (Zalucki et al. 2001a). It is also at this early stage that caterpillars can acquire *Ophryocystis elektroscirrha* from the phylloplane: this neogregarine parasite causes developmental abnormalities during metamorphosis when ingested during the early instars (Leong et al. 1997).

A study examining defensive traits of 24 milkweed species found no trade-offs between defensive traits but instead clustered the species into three defensive strategies: one with low nutritional value, tough leaves, and low water content (i.e., hard to eat, little reward) and two with more nutritious and edible leaves but coupled with either high physical (trichomes, latex) or chemical (cardenolides) defenses. Survival of monarch larvae was similar on all three (Agrawal and Fishbein 2006), suggesting that a complex coevolutionary arms race is operating in this plant-herbivore system.

Experiments in which larvae were reared on leaves with cut laticifers to reduce latex production showed different outcomes on different milkweed species, linked to latex production and cardenolide concentration (Zalucki et al. 2001b, 2012). For instance, *Asclepias humistrata*, one of the main hosts of the first generation of monarchs to reach the southern United States, contains high latex and high cardenolides. Cutting laticifers on this host improved survival (mortality due to miring in the latex was 27% on the intact leaves despite trenching behavior compared with 2% on the notched leaves) and doubled larval growth rate but decreased caterpillar body cardenolide content by half (Zalucki et al. 2001a). However, on the high-latex/low-cardenolide milkweed *Asclepias syriaca*, found in the northern United States and Canada, growth was more rapid on severed-laticifer leaves but survival was unaffected. Neither growth nor survival changed on the low-latex/low-cardenolide *Asclepias incarnata* and *Asclepias tuberosa* (Zalucki et al. 2001b).

Cardenolides consumed by monarch caterpillars are sequestered in body tissues where they appear to protect both larvae and adults from natural enemies and from disease (Malcolm 1994). On *A. syriaca*, a plant with low cardenolide content, larvae protected in cages had a higher survival rate (92%) than larvae left free on plants (24%) (Zalucki et al. 2001b). Adding cardenolides to the artificial diet fed to monarch caterpillars infected with *O. elektroscirrha* slowed parasite growth and increased lifespan of infected but not uninfected butterflies (Gowler et al. 2015). Cardenolide consumption thus appears to mediate a trade-off between toxicity and protection. The production of these compounds is further influenced by yet another trophic level: arbuscular mycorrhizal fungi increase both cardenolides and latex production in infected plants, but the effect on monarch populations is not clear (Tao et al. 2016).

Thus, for neonate monarchs, the first bites into milkweed leaves are dangerous. However, later instars of this specialized herbivore appear better able to circumvent plant chemical and mechanical defenses because their larger mouthparts can more readily cut the laticifers and stop the latex flow (Zalucki et al. 2001b). Plant traits thus play a major role in early-instar survival (Zalucki et al. 2001b), but it is not clear how much this contributes to population dynamics or to the recent decline of North American migratory monarchs.

The main threats causing monarch population declines appear linked to the disappearance of milkweed plants linked to intensive agricultural practices, especially in the US corn belt (Flockhart et al. 2015; Stenoien et al. 2016), although research also suggests declines occurring during migration or on overwintering grounds (Inamine et al. 2016). Summer breeding success does not appear to be affected by changing climate (Stenoien et al. 2016), but monarch populations could be impacted by climate change via increases in extreme weather events during overwintering or reduced rainfall and concomitant decrease in milkweed abundance in the southern spring breeding grounds (Oberhauser et al. 2017). Conservation efforts must focus on the life history stages that affect population dynamics to be effective; for a long-ranging migratory species like the monarch, these can occur thousands of kilometres apart across major biomes and jurisdictions, greatly increasing the challenges of conservation.

Conclusions

Life tables were constructed for many pest insects in the 1960s, often showing very high and very variable early-instar mortality. Further research on several species has shown that neonate caterpillars are indeed very vulnerable, and their survival often depends on phenological relationships with both host plants and natural enemies. The strength, timing, and density dependence of these relationships will determine their effects on population dynamics, suggesting that one needs to consider specific individual-level mechanisms in their ecological context.

For instance, *C. fumiferana* and *C. pinus* share similar ecologies but different population dynamics linked to differences in early-instar mortality (Nealis 2003). A previous section described how early-instar dispersal and mortality in *C. fumiferana* is tied to the availability of buds to emerging larvae, which in turn depends on host phenology and past defoliation.

The congeneric *C. pinus* shares a very similar ecology and life history but very different population dynamics. It also hatches before budbreak of its main host jack pine (*Pinus banksiana* Lamb.), but does not mine old needles and hence depends strongly on the presence of pollen cones for survival. Early-instar survival is 60%–80% when pollen cones are present on the host plant but <10% when they are not. Pollen cone production decreases sharply in accordance with the severity of previous-year defoliation. Lack of pollen cones thus constitutes a lagged density-dependent mortality source that generates the short-lived outbreaks typical of *C. pinus* (Nealis 2003).

Choristoneura fumiferana also mines pollen cones, but because it is also able to mine old foliage, the relationship between early-instar survival and previous defoliation is less strong. Thus, early-instar survivorship and its relationship to host phenology and previous defoliation drives short outbreaks in *C. pinus* and contributes to longer cycles in *C. fumiferana* (Nealis 2003). Explaining the difference in population dynamics between these two species requires an understanding of the relative strengths of the host plant feedbacks affecting the survival of early instars.

Phenological relationships clearly play an important role in early-instar mortality rates, but their contribution to population dynamics is less predictable. For some species, like *C. pinus* as well as *O. brumata* and *Tortrix viridana*, synchrony with the host plant seems to play an important role in generating outbreak cycles via an effect on early-instar survivorship (Nealis 2003). For the four species examined here, the relationship is more complex. Counterintuitively, the role of phenological relationships with host plants in early-instar natural enemy mortality has received little attention, but their effects on late-instar predation rates can be important (e.g., the well-documented slow-growth/high-mortality scenario or the reverse effect observed in gypsy moth (Hunter and Elkinton 2000)).

It is increasingly recognized that phenological tritrophic interactions including host plant, herbivore, and natural enemies create emergent dynamics in herbivore population dynamics (Cooke et al. 2007; Stam et al. 2014). A particularly notable recent development is the realization that the third trophic level includes not only predators and parasitoids but also microbes (Cory and Hoover 2006). Notably, plant compounds that are deemed defensive because of their negative effects on insect performance have recently been shown in several systems to also boost insect immunity, with potentially complex tritrophic feedback effects between plants, herbivores, and pathogens (e.g., gypsy moth (Cory and Hoover 2006), autumnal moth (Kapari et al. 2006), and monarch butterfly (Gowler et al. 2015)). Phenology can drive these relationships in similar ways as with multicellular natural enemies, as insect immunity can vary with host plant synchrony (Martemyanov et al. 2015). The study of mycorrhizae (e.g., Tao et al. 2016), phylloplane flora (e.g., Leong et al. 1997), midgut biota (e.g., Mason and Raffa 2014; Martemyanov et al. 2016), and pathogens (e.g., Hajek et al. 1990; Leong et al. 1997; van Frankenhuyzen et al. 2007; Gowler et al. 2015) in plant–herbivore systems is suggesting potentially important roles for multitrophic interactions with these poorly understood organisms. These relationships are only beginning to be identified and their phenologies or responses to climate have yet to be examined.

In this context, the current paper emphasizes the importance of considering the early-larval instars, despite their small size and general intractability, because of the extremely high and variable mortality that they generally experience and because of their particular sensitivity to phenology and hence to climate change.

Acknowledgements

Thanks to Canada's Natural Sciences and Engineering Research Council for funding and to numerous students and colleagues for help with research underlying this work.

References

Agrawal, A.A. 2012. The monarch–milkweed arms race. *American butterflies, summer 2012*. North American Butterfly Association, Morristown, N.J. pp. 26–27.

Agrawal, A.A., and Fishbein, M. 2006. Plant defense syndromes. *Ecology*, **87**: S132–S149. doi:10.1890/0012-9658(2006)87[132:PDS]2.0.CO;2. PMID:16922309.

Agrawal, A.A., Kearney, E.E., Hastings, A.P., and Ramsey, T.E. 2012. Attenuation of the jasmonate burst, plant defensive traits, and resistance to specialist monarch caterpillars on shaded common milkweed (*Asclepias syriaca*). *J. Chem. Ecol.* **38**: 893–901. doi:10.1007/s10886-012-0145-3. PMID:22661306.

Ammunét, T., Bylund, H., and Jepsen, J.U. 2015. Northern geometrids and climate change: from abiotic factors to trophic interactions. In *Climate change and insect pests*. Edited by C. Björkman and P. Niemelä. CAB International, Wallingford, UK. pp. 235–247. doi:10.1079/9781780643786.0000.

Ayres, M.P., and MacLean, S.F. 1987. Development of birch leaves and the growth energetics of *Epirrita autumnata* (Geometridae). *Ecology*, **68**: 558–568. doi:10.2307/1938461.

Blais, J.R. 1952. The relationship of the spruce budworm (*Choristoneura fumiferana*, Clem.) to the flowering condition of balsam fir (*Abies balsamea* (L.) Mill.). *Can. J. Zool.* **30**(1): 1–29. doi:10.1139/z52-001.

Boggs, C.L. 2016. The fingerprints of global climate change on insect populations. *Curr. Opin. Insect Sci.* **17**: 69–73. doi:10.1016/j.cois.2016.07.004. PMID:27720076.

Bouchard, M., and Auger, I. 2014. Influence of environmental factors and spatio-temporal covariates during the initial development of a spruce budworm outbreak. *Landscape Ecol.* **29**: 111–126. doi:10.1007/s10980-013-9966-x.

Capinera, J.L., and Barbosa, P. 1976. Dispersal of first-instar gypsy moth larvae in relation to population quality. *Oecologia*, **26**: 53–60. doi:10.1007/BF00345652.

Carroll, A.L., and Quiring, D.T. 1994. Intra-tree variation in foliage development influences the foraging strategy of a caterpillar. *Ecology*, **75**: 1978–1990. doi:10.2307/1941602.

Clissold, F.J., Sanson, G.D., Read, J., and Simpson, S.J. 2009. Gross vs. net income: how plant toughness affects performance of an insect herbivore. *Ecology*, **90**: 3393–3405. doi:10.1890/09-0130.1. PMID:20120808.

Cockfield, S.D., and Mahr, D.L. 1993. Consequences of feeding site selection on growth and survival of young blackheaded fireworm (Lepidoptera: Tortricidae). *Environ. Entomol.* **22**: 607–612. doi:10.1093/ee/22.3.607.

Cooke, B., Nealis, V., and Regnière, J. 2007. Insect defoliators as periodic disturbances in northern forest ecosystems. In *Plant disturbance ecology*. 1st ed. Edited by E. Johnson and K. Miyanishi. Academic Press, New York.

Cory, J.S., and Hoover, K. 2006. Plant-mediated effects in insect–pathogen interactions. *Trends Ecol. Evol.* **21**: 278–286. doi:10.1016/j.tree.2006.02.005. PMID:16697914.

Dempster, J.P. 1967. The control of *Pieris rapae* with DDT. I. The natural mortality of the young stages of *Pieris*. *J. Appl. Ecol.* **4**: 485–500.

Despland, E. 2013. Plasticity of collective behavior in a nomadic early spring folivore. *Front. Physiol.* **4**: 54. doi:10.3389/fphys.2013.00054. PMID:23526800.

Dethier, V.G. 1980. The world of the tent-makers: a natural history of the eastern tent caterpillar. University of Massachusetts Press, Amherst, Mass.

Diss, A.L., Kunkel, J.G., Montgomery, M.E., and Leonard, D.E. 1996. Effects of maternal nutrition and egg provisioning on parameters of larval hatch, survival and dispersal in the gypsy moth, *Lymantria dispar* L. *Oecologia*, **106**: 470–477. doi:10.1007/BF00329704.

Dix, M.E., Cunningham, R.A., and King, R.M. 1996. Evaluating spring cankerworm (Lepidoptera: Geometridae) preference for Siberian elm clones. *Environ. Entomol.* **25**: 58–62. doi:10.1093/ee/25.1.58.

Donaldson, J.R., and Lindroth, R.L. 2008. Effects of variable phytochemistry and budbreak phenology on defoliation of aspen during a forest tent caterpillar outbreak. *Agric. For. Entomol.* **10**: 399–410. doi:10.1111/j.1461-9563.2008.00392.x.

Elkinton, J.S., and Liebhold, A.M. 1990. Population dynamics of gypsy moth in North America. *Annu. Rev. Entomol.* **35**: 571–596. doi:10.1146/annurev.en.35.010190.003035.

Erelli, M.C., and Elkinton, J.S. 2000. Factors influencing dispersal in neonate gypsy moths (Lepidoptera: Lymantriidae). *Environ. Entomol.* **29**: 509–515. doi:10.1603/0046-225X-29.3.509.

Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology*, **51**: 565–581. doi:10.2307/1934037.

Floater, G.J., and Zalucki, M.P. 1999. Life tables of the processionary caterpillar *Ochrogaster lunifer* Herrich-Schaffer (Lepidoptera: Thaumetopoeidae) at local and regional scales. *Aust. J. Entomol.* **38**: 330–339. doi:10.1046/j.1440-6055.1999.00122.x.

Flockhart, D.T.T., Pichancourt, J.B., Norris, D.R., and Martin, T.G. 2015. Unravelling the annual cycle in a migratory animal: breeding-season habitat loss drives population declines of monarch butterflies. *J. Anim. Ecol.* **84**: 155–165. doi:10.1111/1365-2656.12253. PMID:24903085.

Foster, J.R., Townsend, P.A., and Mladenoff, D.J. 2013. Mapping asynchrony between gypsy moth egg-hatch and forest leaf-out: putting the phenological window hypothesis in a spatial context. *For. Ecol. Manage.* **287**: 67–76. doi:10.1016/j.foreco.2012.09.006.

Fuentealba Morales, A., Pureswaran, D.S., Bauce, E., and Despland, E. 2017. How does synchrony with host plant affect spruce budworm performance? *Oecologia*. Submitted.

Girón-Calva, P.S., Li, T., Koski, T.M., Klemola, T., Laaksonen, T., Huttunen, L., and Blande, J.D. 2014. A role for volatiles in intra- and inter-plant interactions in birch. *J. Chem. Ecol.* **40**: 1203–1211. doi:10.1007/s10886-014-0514-1. PMID:25352241.

Gowler, C.D., Leon, K.E., Hunter, M.D., and de Roode, J.C. 2015. Secondary defense chemicals in milkweed reduce parasite infection in monarch butterflies, *Danaus plexippus*. *J. Chem. Ecol.* **41**: 520–523. doi:10.1007/s10886-015-0586-6. PMID:25953502.

Hajek, A.E., Humber, R.A., Elkinton, J.S., May, B., Walsh, S.R., and Silver, J.C. 1990. Allozyme and restriction fragment length polymorphism analyses confirm *Entomophaga maimaiga* responsible for 1989 epizootics in North American gypsy moth populations. *Proc. Natl. Acad. Sci. U.S.A.* **87**: 6979–6982. doi:10.1073/pnas.87.18.6979. PMID:11607100.

Haukioja, E. 2003. Putting the insect into the birch–insect interaction. *Oecologia*, **136**: 161–168. doi:10.1007/s00442-003-1238-z. PMID:12684856.

Haukioja, E. 2005. Plant defenses and population fluctuations of forest defoliators: mechanism-based scenarios. *Ann. Zool. Fenn.* **42**: 313–325.

Hawkins, B.A., Cornell, H.V., and Hochberg, M.E. 1997. Predators, parasitoids, and pathogens as mortality agents in phytophagous insect populations. *Ecology*, **78**: 2145–2152. doi:10.1890/0012-9658(1997)078[2145:PPAPAM]2.0.CO;2.

Hayes, J.L. 1981. The population ecology of a natural population of the pierid butterfly *Colias alexandra*. *Oecologia*, **49**: 188–200. doi:10.1007/BF00349187.

Hochuli, D.F. 2001. Insect herbivory and ontogeny: how do growth and development influence feeding behaviour, morphology and host use? *Austral Ecol.* **26**: 563–570. doi:10.1046/j.1442-9993.2001.01135.x.

Hunter, A.F. 1993. Gypsy moth population sizes and the window of opportunity in spring. *Oikos*, **68**: 531–538.

Hunter, A.F., and Elkinton, J.S. 2000. Effects of synchrony with host plant on populations of a spring-feeding lepidopteran. *Ecology*, **81**: 1248–1261. doi:10.1890/0012-9658(2000)081[1248:EOSWHP]2.0.CO;2.

Inamine, H., Ellner, S.P., Springer, J.P., and Agrawal, A.A. 2016. Linking the continental migratory cycle of the monarch butterfly to understand its population decline. *Oikos*, **125**: 1081–1091. doi:10.1111/oik.03196.

Johns, R.C., and Eveleigh, E.S. 2013. Ontogeny and stand condition influence the dispersal behavior of a defoliating specialist caterpillar. *Environ. Entomol.* **42**: 1329–1337. doi:10.1603/EN13083. PMID:24216325.

Johnson, M.-L., and Zalucki, M.P. 2007. Feeding and foraging behaviour of a generalist caterpillar: are third instars just bigger versions of firsts? *Bull. Entomol. Res.* **97**: 81–88. doi:10.1017/S0007485307004750. PMID:17298685.

Kaitaniemi, P., and Ruohomäki, K. 1999. Effects of autumn temperature and

- oviposition date on timing of larval development and risk of parasitism in a spring folivore. *Oikos*, **84**: 435–442. doi:10.2307/3546422.
- Kapari, L., Haukioja, E., Rantala, M.J., and Ruuhola, T. 2006. Defoliating insect immune defense interacts with induced plant defense during a population outbreak. *Ecology*, **87**: 291–296. doi:10.1890/05-0362. PMID:16637353.
- Klemola, T., Ammunet, T., Andersson, T., Klemola, N., and Ruohomäki, K. 2012. Larval parasitism rate increases in herbivore-damaged trees: a field experiment with cyclic birch feeding moths. *Oikos*, **121**: 1525–1531. doi:10.1111/j.1600-0706.2011.20096.x.
- Klemola, T., Andersson, T., and Ruohomäki, K. 2014. Delayed density-dependent parasitism of eggs and pupae as a contributor to the cyclic population dynamics of the autumnal moth. *Oecologia*, **175**: 1211–1225. doi:10.1007/s00442-014-2984-9. PMID:24958367.
- Kursar, T.A., and Coley, P.D. 2003. Convergence is defense syndromes of young leaves in tropical rainforests. *Biochem. Syst. Ecol.* **31**: 929–949.
- Lahtinen, M., Salminen, J.-P., Kapari, L., Lempa, K., Ossipov, V., Sinkkonen, J., Valkama, E., Haukioja, E., and Pihlaja, K. 2004. Defensive effect of surface flavonoid aglycones of *Betula pubescens* leaves against first instar *Epirrita autumnata* larvae. *J. Chem. Ecol.* **30**: 2257–2268. doi:10.1023/B:JOEC.0000048787.34388.dd. PMID:15672669.
- Lahtinen, M., Kapari, L., and Kenttä, J. 2006. Newly hatched neonate larvae can glycosylate: the fate of *Betula pubescens* bud flavonoids in first instar *Epirrita autumnata*. *J. Chem. Ecol.* **32**: 537–546. doi:10.1007/s10886-005-9015-6. PMID:16572299.
- Lawrence, R.K., Mattson, W.J., and Haack, R.A. 1997. White spruce and the spruce budworm: defining the phenological window of susceptibility. *Can. Entomol.* **129**: 291–318. doi:10.4039/Ent129291-2.
- Leonard, D.E. 1970a. Effects of starvation on behavior, number of larval instars and developmental rate of *Porthetria dispar*. *J. Insect Physiol.* **16**: 25–31. doi:10.1016/0022-1910(70)90109-5.
- Leonard, D.E. 1970b. Intrinsic factors causing qualitative changes in populations of *Porthetria dispar* (Lepidoptera: Lymantriidae). *Can. Entomol.* **102**: 239–249. doi:10.4039/Ent102239-2.
- Leong, K.L.H., Yoshimura, M.A., Kaya, H.K., and Williams, H. 1997. Instar susceptibility of the monarch butterfly (*Danaus plexippus*) to the neogregarine parasite, *Ophryocystis elektroscirrha*. *J. Invertebr. Pathol.* **69**: 79–83. doi:10.1006/jip.1996.4634. PMID:9028932.
- Malcolm, S.B. 1994. Milkweeds, monarch butterflies and the ecological significance of cardenolides. *Chemoecology*, **5**–6: 101–117. doi:10.1007/BF01240595.
- Martemyanov, V.V., Pavlushin, S.V., Dubovskiy, I.M., Yushkova, Y.V., Morosov, S.V., Chernyak, E.I., Efimov, V.M., Ruuhola, T., and Glupov, V.V. 2015. Asynchrony between host plant and insects-defoliator within a tritrophic system: the role of herbivore innate immunity. *PLoS One*, **10**: e0130988. doi:10.1371/journal.pone.0130988. PMID:26115118.
- Martemyanov, V.V., Belousova, I.A., Pavlushin, S.V., Dubovskiy, I.M., Ershov, N.I., Alikina, T.Y., Kabilov, M.R., and Glupov, V.V. 2016. Phenological asynchrony between host plant and gypsy moth reduces insect gut microbiota and susceptibility to *Bacillus thuringiensis*. *Ecol. Evol.* **6**: 7298–7310. doi:10.1002/ece3.2460.
- Mason, C.J., and Raffa, K.F. 2014. Acquisition and structuring of midgut bacterial communities in gypsy moth (Lepidoptera: Erebidae) larvae. *Environ. Entomol.* **43**: 595–604. doi:10.1603/EN14031. PMID:24780292.
- Nealis, V.G. 2003. Host–plant relationships and comparative ecology of conifer-feeding budworms (*Choristoneura* spp.). In *Ecology, survey and management of forest insects*. USDA For. Serv. Gen. Tech. Rep. NE-311, Northeastern Research Station. pp. 68–74.
- Nixon, A.E., and Roland, J. 2012. Generalist predation on forest tent caterpillar varies with forest stand composition: an experimental study across multiple life stages. *Ecol. Entomol.* **37**: 13–23. doi:10.1111/j.1365-2311.2011.01330.x.
- Oberhauser, K., Wiederholt, R., Diffendorfer, J.E., Semmens, D., Ries, L., Thogmartin, W.E., Lopez-Hoffman, L., and Semmens, B. 2017. A transnational monarch butterfly population model and implications for regional conservation priorities. *Ecol. Entomol.* **42**: 51–60. doi:10.1111/een.12351.
- Ossipov, V., Klemola, T., Ruohomäki, K., and Salminen, J.-P. 2014. Effects of three years' increase in density of the geometrid *Epirrita autumnata* on the change in metabolome of mountain birch trees (*Betula pubescens* ssp. *czerepanovii*). *Chemoecology*, **24**: 201–214. doi:10.1007/s00049-014-0164-3.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Syst.* **37**: 637–669. doi:10.1146/annurev.ecolsys.37.091305.110100.
- Parry, D., Spence, J.R., and Volney, W.J.A. 1998. Budbreak phenology and natural enemies mediate survival of first-instar forest tent caterpillar (Lepidoptera: Lasiocampidae). *Environ. Entomol.* **27**: 1368–1374. doi:10.1093/ee/27.6.1368.
- Perkins, L., Cribb, B., Hanan, J., and Zalucki, M. 2008. Where to from here? The mechanisms enabling movement of *Helicoverpa armigera* (Hübner) first instar larvae on pea plants. *Arthropod-Plant Interact.* **2**: 197–207.
- Pureswaran, D.S., De Grandpré Paré, L., Taylor, D., Barrette, A., Morin, M., Régnière, H., Kneeshaw, J., D.D. 2015. Climate-induced changes in host tree-insect phenology may drive ecological state-shift in boreal forests. *Ecology*, **96**: 1480–1491. doi:10.1890/13-2366.1.
- Rathcke, B.J., and Poole, R.W. 1975. Coevolutionary race continues: butterfly larval adaptation to plant trichomes. *Science*, **187**: 175–176. doi:10.1126/science.187.4172.175. PMID:17736541.
- Régnière, J., and Nealis, V.G. 2007. Ecological mechanisms of population change during outbreaks of the spruce budworm. *Ecol. Entomol.* **32**: 461–477. doi:10.1111/j.1365-2311.2007.00888.x.
- Régnière, J., and Nealis, V.G. 2008. The fine-scale population dynamics of spruce budworm: survival of early instars related to forest condition. *Ecol. Entomol.* **33**: 362–373. doi:10.1111/j.1365-2311.2007.00977.x.
- Richardson, M.L., Mitchell, R.F., Reagal, P.F., and Hanks, L.M. 2010. Causes and consequences of cannibalism in noncarnivorous insects. *Annu. Rev. Entomol.* **55**: 39–53. doi:10.1146/annurev-ento-112408-085314. PMID:19961322.
- Riipi, M., Ossipov, V., Lempa, K., Haukioja, E., Koricheva, J., Ossipova, S., and Pihlaja, K. 2002. Seasonal changes in birch leaf chemistry: are there trade-offs between leaf growth and accumulation of phenolics? *Oecologia*, **130**: 380–390. doi:10.1007/s00442-001-0826-z.
- Rossiter, M.C. 1991. Environmentally-based maternal effects: a hidden force in insect population dynamics? *Oecologia*, **87**: 288–294. doi:10.1007/BF00325268.
- Royama, T. 1984. Population dynamics of the spruce budworm *Choristoneura fumiferana*. *Ecol. Monogr.* **54**: 429–462. doi:10.2307/1942595.
- Ruohomäki, K., Tanhuanpää, M., Ayres, M.P., Kaitaniemi, P., Tammaru, T., and Haukioja, E. 2000. Causes of cyclicity of *Epirrita autumnata* (Lepidoptera, Geometridae): grandiose theory and tedious practice. *Popul. Ecol.* **42**: 211–223. doi:10.1007/PL00012000.
- Ruuhola, T., Yang, S., Ossipov, V., and Haukioja, E. 2008. Foliar oxidases as mediators of the rapidly induced resistance of mountain birch against *Epirrita autumnata*. *Oecologia*, **154**: 725–730. doi:10.1007/s00442-007-0869-x. PMID:17952472.
- Schmitz, O.J., Krivan, V., and Ovadia, O. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol. Lett.* **7**: 153–163. doi:10.1111/j.1461-0248.2003.00560.x.
- Scriber, J.M., and Slansky, F., Jr. 1981. The nutritional ecology of immature insects. *Annu. Rev. Entomol.* **26**: 183–211. doi:10.1146/annurev.en.26.010181.001151.
- Smiley, J.T. 1985. *Heliconius* caterpillar mortality during establishment on plants with and without attending ants. *Ecology*, **66**: 845–849. doi:10.2307/1940546.
- Sonntag, P. 2016. Attack of the budworms. *The Walrus*, 15 November.
- Stam, J.M., Kroes, A., Li, Y., Gols, R., van Loon, J.J.A., Poelman, E.H., and Dicke, M. 2014. Plant interactions with multiple insect herbivores: from community to genes. *Annu. Rev. Plant Biol.* **65**: 689–713. doi:10.1146/annurev-arplant-050213-035937. PMID:24313843.
- Stenoien, C., Nail, K.R., Zalucki, J.M., Parry, H., Oberhauser, K.S., and Zalucki, M.P. 2016. Monarchs in decline: a collateral landscape-level effect of modern agriculture. *Insect Sci.* doi:10.1111/1744-7917.12404.
- Tanhuanpää, M., Ruohomäki, K., and Uusipaikka, E. 2001. High larval predation rate in non-outbreaking populations of a geometrid moth. *Ecology*, **82**: 281–289. doi:10.1890/0012-9658(2001)082[0281:HLPRIJ]2.0.CO;2.
- Tao, L., Ahmad, A., de Roode, J.C., and Hunter, M.D. 2016. Arbuscular mycorrhizal fungi affect plant tolerance and chemical defences to herbivory through different mechanisms. *J. Ecol.* **104**: 561–571. doi:10.1111/1365-2745.12535.
- Trier, T.M., and Mattson, W.J. 1997. Needle mining by the spruce budworm provides sustenance in the midst of privation. *Oikos*, **79**: 241–246. doi:10.2307/3546009.
- van Asch, M., and Visser, M.E. 2007. Phenology of forest caterpillars and their host trees: the importance of synchrony. *Annu. Rev. Entomol.* **52**: 37–55. doi:10.1146/annurev.ento.52.110405.091418. PMID:16842033.
- van Frankenhuyzen, K., Nystrom, C., and Liu, Y. 2007. Vertical transmission of *Nosema fumiferanae* (Microsporidia: Nosematidae) and consequences for distribution, post-diapause emergence and dispersal of second-instar larvae of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). *J. Invertebr. Pathol.* **96**: 173–182. doi:10.1016/j.jip.2007.03.017. PMID:17512004.
- Westgard, P.H., Gentner, L., and Butt, B.A. 1976. Codling moth: egg and first instar mortality on pear with special reference to varietal susceptibility. *Environ. Entomol.* **5**: 51–54. doi:10.1093/ee/5.1.51.
- Zalucki, M.P., Brower, L.P., and Alonso, A. 2001a. Detrimental effects of latex and cardiac glycosides on survival and growth of first-instar monarch butterfly larvae *Danaus plexippus* feeding on the sandhill milkweed *Asclepias humistrata*. *Ecol. Entomol.* **26**: 212–224. doi:10.1046/j.1365-2311.2001.00313.x.
- Zalucki, M.P., Malcolm, S.B., Paine, T.D., Hanlon, C.C., Brower, L.P., and Clarke, A.R. 2001b. It's the first bites that count: survival of first-instar monarchs on milkweeds. *Austral Ecol.* **26**: 547–555. doi:10.1046/j.1442-9993.2001.01132.x.
- Zalucki, M.P., Clarke, A.R., and Malcolm, S.B. 2002. Ecology and behavior of first instar larval lepidoptera. *Annu. Rev. Entomol.* **47**: 361–393. doi:10.1146/annurev.ento.47.091201.145220. PMID:11729079.
- Zalucki, M.P., Malcolm, S.B., Hanlon, C.C., and Paine, T.D. 2012. First-instar monarch larval growth and survival on milkweeds in southern California: effects of latex, leaf hairs and cardenolides. *Chemoecology*, **22**: 75–88. doi:10.1007/s00049-011-0099-x.
- Zhan, S., Zhang, W., Niitepöld, K., Hsu, J., Haeger, J.F., Zalucki, M.P., Altizer, S., de Roode, J.C., Reppert, S.M., and Kronforst, M.R. 2014. The genetics of monarch butterfly migration and warning colouration. *Nature*, **514**: 317–321. doi:10.1038/nature13812. PMID:25274300.