

Ecology of outbreak populations of the western spruce budworm

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Abstract. We sampled outbreak populations of western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae), between 1997 and 2016 in Douglas-fir forests in the interior of British Columbia, Canada. Annual rates of change in population densities were correlated with generation survival, modulated by egg recruitment via dispersal of moths. Most temporal variation in generation survival was the result of variation in survival of small, non-feeding larval stages. Survival rates of feeding larval and pupal stages determined the magnitude of generation survival but contributed little to temporal trend. Survival of small larvae was the product of density-related losses of larvae dispersing to and from hibernation sites and weather-related stress caused by warm temperatures in late summer and early spring. Overwinter survival improved in cooler years and at higher elevations. Survival of feeding larvae and pupae was associated with mortality by natural enemies, in particular a few species of dominant, ubiquitous endoparasitoids, and an episodic, virulent baculovirus. Recruitment of eggs indicated emigration of gravid moths independent of defoliation but proportional to density of local moths. During periods of increasing and decreasing population densities over a large outbreak area, a marked differential in adult densities among locations resulted in greater than expected per-capita egg recruitment to areas of relatively low density and vice versa, indicative of net exchange of gravid moths from high- to low-density populations. The result was homogenization of egg densities among locations, apparent synchrony of the outbreak at the large scale, and extended duration of the outbreak at some locations, despite declining generation survival. These results are compared with field studies of the closely related spruce budworm, *Choristoneura fumiferana*. We suggest our interpretation applies more generally and outbreaks of conifer-feeding budworms are maintained for several years by compensatory survival of sequential life-history stages and spatio-temporal smoothing of densities via dispersal of gravid moths. Parasitoids and pathogens can cause sudden declines in densities, but populations inevitably wane as a result of cumulative degradation of their resource. The interaction and temporal sequence of bottom-up and top-down factors explain the similarities and differences in outbreak characteristics within- and among-budworm species.

Key words: dispersal; natural enemies; population dynamics; recruitment; survival; weather; western spruce budworm.

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INTRODUCTION

The ecology of periodic, irruptive forest insects is a rich field in animal population dynamics.

The grand scale of outbreaks has resulted in compilation of records on their timing, location, amplitude and duration, and a considerable amount of research on causal mechanisms. This

research has been motivated largely by interest in forest resource management but has also informed fundamental concepts in ecological theory including density dependence, population stability, equilibrium (Royama 1992, Berryman and Kindlmann 2008), and resilience (Holling 1973), as well as the complex outcomes of trophic interactions (Berryman 2002, Cooke et al. 2020).

Among the most studied forest defoliators are conifer-feeding budworms in the genus *Choristoneura*. The most prominent species native to North American forests, spruce budworm (*Choristoneura fumiferana* Clemens), jack pine budworm (*Choristoneura pinus pinus* Freeman), and western spruce budworm (*Choristoneura occidentalis* Freeman), have near-identical life histories but exploit different tree species in distinct biogeographic ecozones. Their historic outbreak dynamics also differ in periodicity, extent, and duration (Nealis 2016). Recent outbreaks of all species have occurred in novel locations of their extensive ranges (Bouchard and Auger 2014, Hughes et al. 2014, Maclauchlan et al. 2018), indicating recent, large-scale geographic changes in climatic conditions are influencing contemporary dynamics (Régnière et al. 2012b, Régnière and Nealis 2019a).

First-hand, scientific accounts of outbreaks of the spruce budworm, *C. fumiferana*, are available since early in the 20th century (Craighead 1924). The Green River Project in New Brunswick, Canada, emerged as the foundational study on the dynamics of outbreaks (Morris 1963a). The project was notable for its application of basic ecology to management of a significant forest pest (Clarke et al. 1979) and launched a continuing debate on the dynamics of outbreaks (Pureswaran et al. 2016, Régnière et al. 2019). Two contrasting theories emerged. A qualitative analysis distilled from detailed simulation models characterized spruce budworm dynamics as a rapid oscillation between low and high, locally stable, population densities (Ludwig et al. 1978). Budworm survival increased during periods of favorable forest and weather conditions, outpacing attack rates of natural enemies. As populations irrupted, dispersal of egg-bearing moths amplified increases elsewhere, causing an epidemic. Eventually, populations collapsed abruptly via the combined effects of forest depletion and natural enemies.

Royama (1984) applied new analytical methods directly to field data from the Green River

Project and rejected the multiple equilibrium hypothesis. He concluded rates of change in density were continuous with no evidence of long-term stasis or equilibria. Gradual change in population density was the result of local processes; specifically, an intrinsic, primary oscillation caused by regionally correlated fluctuations in generation survival. The principal cause of these trends was survival of the feeding larval and pupal stages, largely determined by natural enemies. The action of these top-down forces aligned with classical predator–prey relationships in which cyclical population behavior results from lagged, density-dependent interactions between trophic levels (Royama 1992).

A new generation of field studies beginning in the 1980s confirmed the important role of natural enemies attacking late-stage larvae (Régnière and Nealis 2007, Royama et al. 2017), but also found damage-related changes in host condition negatively affected survival of early-stage larvae (Régnière and Nealis 2008). A lagged, density-dependent relationship between feeding damage and survival, identified for the jack pine budworm (Nealis et al. 2003), illustrated how such fine-scale, bottom-up ecological relationships cause marked variation in outbreak behavior (Régnière and Nealis 2008). These density-dependent impacts of changing forest condition on budworm survival at variable ecological scales were proposed as a general feature in the dynamics of irruptive forest defoliators (Nealis 2016, Cooke et al. 2020).

There are few longitudinal studies comparable to those of spruce budworm available for other forest defoliators to evaluate the generality of hypotheses. Campbell (1993) assembled several short-term data sets from outbreak populations of the western spruce budworm in the USA, identified a set of variables suspected of influencing dynamics, and compared his results to population studies available for spruce and jack pine budworms. He challenged the view of Royama (1984) that budworm dynamics was a spatially congruent phenomenon dominated by local events associated with only a few life stages. In western spruce budworm, he found evidence of diverse, density-related survival patterns and hypothesized that both synchrony and duration of regional outbreaks were the result of moth dispersal.

We applied field methods developed for spruce budworm populations to the western spruce budworm during a recent outbreak (1996–2016) in the interior of British Columbia (BC), Canada. Several detailed, process-oriented studies were published enroute. These studies revealed significant relationships between survival of small western spruce budworm larvae and damage-related changes in forest condition (Nealis and Régnière 2009), survival of feeding larvae and seasonal changes in quality of host foliage (Nealis 2012), and fitness over the entire generation resulting from spatial-temporal variation in the phenological window for feeding, maturation, and reproduction (Régnière and Nealis 2019a). Location-specific patterns of overwinter survival (Nealis and Régnière 2016) and direct evidence of density-related dispersal of gravid moths affecting local rates of recruitment (Régnière and Nealis 2019b) were also quantified.

This paper integrates the results of these process studies with time series of the density, stage-specific survival, and recruitment of western spruce budworms over the duration of an outbreak at a regional scale. We hypothesize that density-related factors involving producer, consumer, and natural enemy trophic levels affect budworm survival at several points in the life cycle. The strength of these trophic relationships, and therefore population outcomes of the interactions, vary at spatial and temporal scales, and so require field data of sufficient extent and duration to detect. Results are discussed in terms of the irruptive dynamics of related forest defoliators and the extent to which stage-specific, density-related factors interact to enhance and compensate patterns of survival at local and regional scales. Finally, we touch on the implications of our results for management of the western spruce budworm and potential changes in population behavior resulting from climate change.

METHODS

Western spruce budworm

The western spruce budworm is distributed between approximately 32° and 53° N, westward from the foothill forests of the Rocky Mountains to the Pacific Coast of North America. Principal

hosts over this extensive range are Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), true firs (*Abies*), and to a lesser extent, Engelmann spruce (*Picea engelmannii* Parry ex Engelm.). In the northern part of the western spruce budworm's range, specifically Western Canada (>49° N), Douglas-fir is essentially the exclusive host as *Abies* and *Picea* at these latitudes are characteristics of higher elevations where two-year cycle spruce budworm, *C. occidentalis biennis* (Freeman), has been most common historically (Nealis 2016).

Dendroecological records suggest western spruce budworm populations have erupted on a regional scale at 30- to 40-yr intervals for at least 400 yr (Swetnam and Lynch 1993, Alfaro et al. 2014, Axelson et al. 2015). The earliest direct observations of defoliation in BC were early in the 20th century when small areas of damage occurred in the south-coastal range (Harris et al. 1985). Subsequent outbreaks in BC have been increasingly extensive with peaks in area of defoliation recorded in 1976, 1987, and 2007, concentrated in southern and central interior forests (Fig. 1).

A generation of western spruce budworm has five, ecologically distinct life-history stages: (1) eggs (E); (2) small, non-feeding larvae (L_{1-2}); (3) large, feeding larvae (L_{3-6}); (4) pupae (P); and (5) adults (M). Moths lay eggs in masses of 25–50 eggs on host foliage from mid-July to mid-August in BC. Neonate larvae (L_1) hatch in about one week. They disperse immediately from the egg mass and settle in shelters throughout the tree where they construct hibernacula, molt to a second instar (L_2), and spend the remaining summer, autumn, and most of winter in diapause. By late February, diapause ends and larvae become responsive to warm temperatures (Nealis and Régnière 2014), but remain dormant until mid-May or early June when warmer spring weather conditions permit emergence (Nealis and Nault 2005). The emergence period is in advance of availability of current-year buds so small larvae forage throughout the canopy, sustained by mining previous years' needles or fresh pollen cones, when available. Most mortality during this lengthy, non-feeding period is the result of losses of small larvae associated with finding winter shelter, enduring variable environmental conditions for nine months without feeding (Nealis

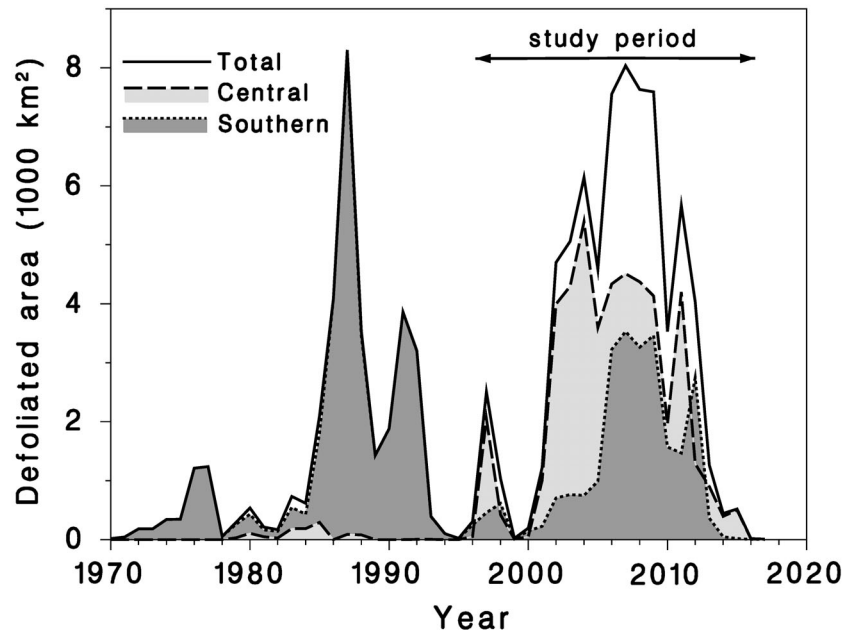


Fig. 1. Area (ha) defoliated by the western spruce budworm in southern and central interior of British Columbia (Fig. 2; south and north of the Thompson River, respectively) since 1970. Data to 1995 from Forest Insect and Disease Survey (Natural Resources Canada) and thereafter from <https://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/forest-health/aerial-overview-surveys/summary-reports>.

and Régnière 2016), and then foraging for feeding sites in the spring, again influenced by the physical environment including host and stand conditions (Nealis and Régnière 2009).

Once small larvae settle in expanding current-year buds, the maturation feeding period (L_3 – L_6) begins, ending with pupation (P). Important mortality factors during the feeding larval and pupal periods are natural enemies (Nealis et al. 2009, 2015). Adult moths (M) emerge approximately one week after pupation, mate, lay at least some eggs in their natal site, and then may migrate many kilometers, depending on weather conditions.

A western spruce budworm generation spans two calendar-years. We designate year t as the calendar-year in which budworm larvae emerge from hibernacula, feed, and mature to adult. Accordingly, a budworm generation begins with eggs laid in calendar-year $t - 1$ and surviving adults emerge in year t . Recruitment of eggs to the next generation, $t + 1$, occurs when adults of year t lay eggs initiating the next generation. The inter-generation rate of change is the ratio of a

life stage density in year t to the density of the same stage in the previous year $t - 1$. Thus, in our scheme, nominal generation and calendar-years are the same. All graphs with temporal axes represent calendar-year t unless otherwise noted.

Study locations

The area and period covered by this study (Figs. 1, 2) were fortuitous insofar as they document the most extensive and prolonged recorded outbreak of western spruce budworm in this northern portion of its range. Population data were collected between 1997 and 2016 from 30 locations spanning the elevation and latitude ranges of the Interior Douglas-fir biogeoclimatic zone of BC, for a total of 241 plot-years. Seven primary study locations, sampled for up to 21 generations, were situated along elevation transects from 600 to 1350 m in the Nicola and Okanagan valleys (Fig. 2; blue and red symbols, respectively). Surveys first recorded defoliation in the Okanagan Valley in the late-1970s (Harris et al. 1985), and the area became part of the

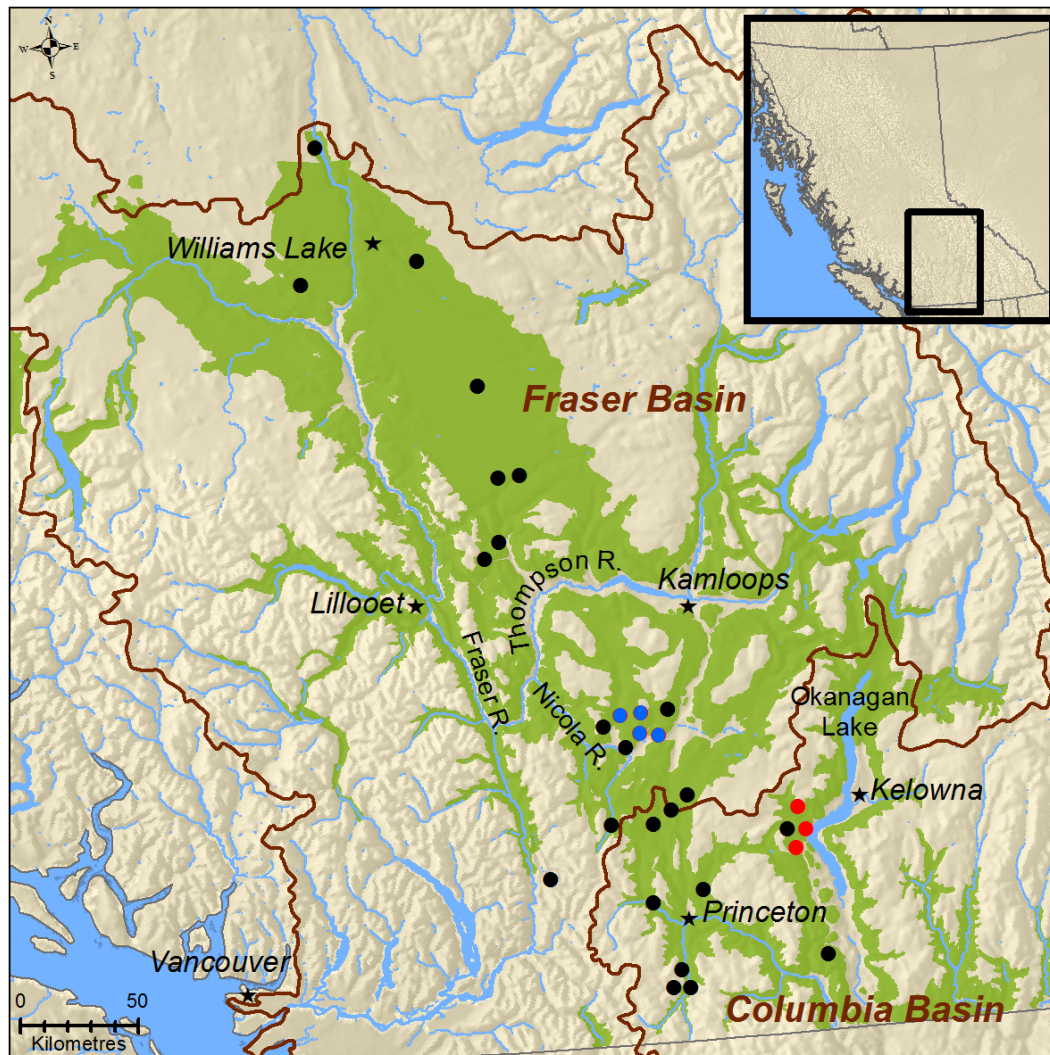


Fig. 2. Study locations (red circles, Okanagan Valley primary; blue circles, Nicola Valley primary; black circles, secondary) in Interior Douglas-fir zone of British Columbia, Canada (green). Brown borders are boundaries of Fraser and Columbia River Basins.

larger outbreak in the 1980s (Parfett et al. 1994). Populations at these locations were decreasing at the beginning of this study (Figs. 1, 3e–g). There was little to no defoliation recorded in the Nicola Valley near primary study locations until 1997 when sampling began, so our study covers most of the outbreak period at these locations.

Study locations are representative of mature, interior Douglas-fir stands. Stand-level statistics for the seven primary locations plus two others were derived from measurement of all Douglas-fir trees in 10 fixed-radius circular plots (radii =

3.99 or 5.64 m) at 25-m intervals along U-shaped transects at each location. Measurement of DBH (diameter at breast height) and height of trees with a DBH ≥ 10 cm allowed calculation of total biomass of Douglas-fir foliage per ha, Ψ (metric tons/ha; Nealis and Régnière 2009). Douglas-fir trees < 10 cm DBH and ≥ 1 m in height and non-host tree species in the circular plots with a DBH ≥ 10 cm were counted. Initial measurements were made in either 1997 or 2004, and the same co-dominant trees in both sets re-measured in 2011 and tree mortality recorded. No additional

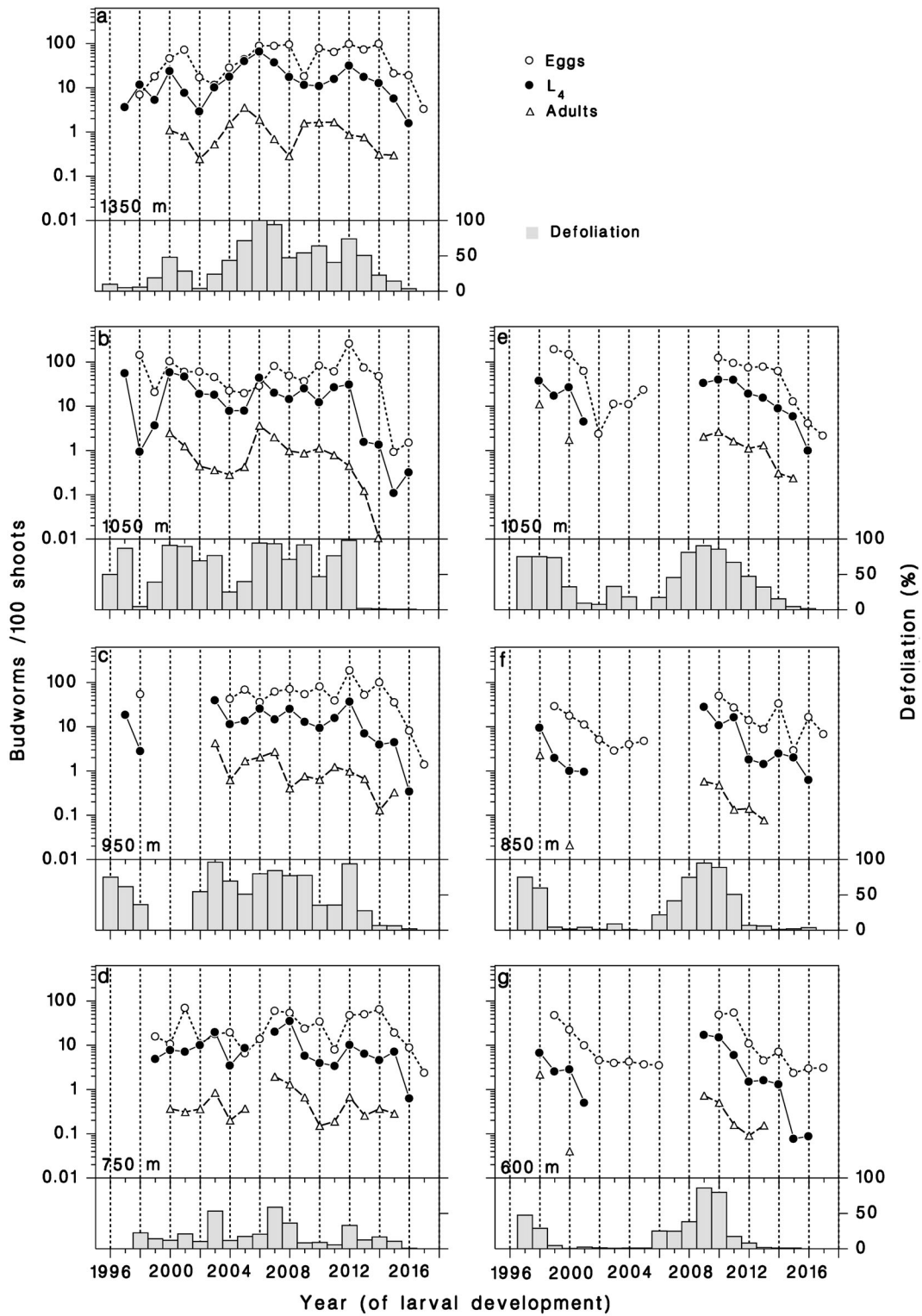


Fig. 3. Mean density (per 100 shoots) in the egg, early-feeding larval (L₄), and adult stages of western spruce

(Fig. 3. *Continued*)

budworm, and annual defoliation (D_i , %) at seven primary study locations in the Nicola (left column) and Okanagan (right column) valleys in British Columbia, Canada, between 1997 and 2016. (a) Pentangle; (b) Kirby; (c) Steffens; (d) Clapperton; (e) Coldham; (f) Pine Ridge; and (g) Peachland.

mortality to co-dominant sample trees in primary sample locations was noted during final sampling in 2016.

The 23 secondary study locations were between 800 and 1250 m, extending from the Canada–USA border (49° N) north to 52°5' N, near the northern range limit of Douglas-fir (Fig. 2; black dots). Thirteen of these locations were sampled from four to nine years as part of a forest management investigation (Nealis et al. 2009) and the rest for one or two years during surveys for pathogens of the western spruce budworm (Nealis et al. 2015).

Sampling western spruce budworm and their damage

Basic field sampling methods developed for spruce budworm (Morris 1955) were used for western spruce budworm populations (Nealis et al. 2009). The sample unit was a 45-cm branch tip removed from the mid-crown of each of 10 co-dominant Douglas-fir trees per location using extendable poles equipped with a cutting head and a basket to catch the foliage. Campbell et al. (1984) confirmed this sample unit was representative of densities of life stages of western spruce budworm on Douglas-fir. Two branches were taken from each tree. With few exceptions, we sampled populations at least three times per generation: (1) eggs (E) in late summer after oviposition and hatch were complete, (2) fourth instar (L_4) in spring when all surviving budworms had emerged from hibernacula and established feeding sites, and (3) late-stage larvae (L_6) and pupae (P) in mid-summer when budworms reached the end of their feeding period and were pupating.

The fresh weight of each branch was recorded and all budworms removed, enumerated, and assigned an age class based on measurement of head-capsules for larvae, full pupae, pupal exuviae (adults), or eggs. Branch area (sample length by widest point divided by 2) and counts of current-year buds were recorded on subsamples, allowing alternative expressions of relative density

of insects. Because the number of buds per kg of host foliage in conifers varies with previous defoliation (Nealis and Régnière 2004a), we express the density of budworm in life stage i as the mean number of insects per 100 buds, n_i . This expression relates the insect directly to the available resource and accommodates the defoliation-related changes to the food source over time (Appendix S1). Average instar, α_i , summarizes the distribution of life stages at each sample date (Hardy et al. 1976). From these samples, we obtained six successive estimates of population density:

1. n_1 The density of eggs (E) was the recorded number of egg masses times the mean number of eggs per mass estimated from a subset of egg masses from each location-year. When there were fewer than 10 egg masses available for a location, the overall mean (SEM), 28.5 (± 0.15) eggs per mass, was used;
2. n_2 The density of neonates (L_1) was n_1 minus the observed number of eggs parasitized by *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae);
3. n_3 The density of second-instar larvae (L_2) successfully completing winter diapause and emerging in the spring was calculated directly for some location-years (Nealis and Régnière 2009) and calculated for others using estimates of overwinter survival (see *Analysis*);
4. n_4 The density of larvae at the beginning of the feeding stage (nominal L_4) was estimated in spring once budworms had emerged and become established in feeding sites. Whenever repeated sampling occurred during this period, we used the maximum density estimate observed in the series (Royama et al. 2017). Mean (\pm SEM) average instar among these samples in all locations was $\alpha = 3.88 (\pm 0.046)$, $n = 156$;
5. n_5 The density of pupae (P) was estimated at the end of the active feeding period. During the transition from larva to pupa, average

instar varied among locations at a given sample date within any one year. We sampled locations weekly until the populations approached 50% pupation, at least. Only cohorts with $\alpha \geq 5.2$ were included in analysis. Otherwise, we considered a late-season sample missing. Mean (\pm SEM) average instar for this cohort was $\alpha = 6.21$ (0.054), $n = 121$;

6. n_6 The density of adults (A) was the sum of observed number of adults (i.e., pupal exuviae) in the sample and the observed number of pupae in the sample that would have survived to adult as determined from rearing survival (see *Rearing cohorts for natural enemies*). This is an overestimate as it does not account for additional mortality of immature stages after the last sample date. The magnitude of this bias is a function of the age distribution of budworms in the last sample and survival of that cohort to adult, so a correction could be calculated from sampling and rearing data to obtain unbiased estimates of n_6 (Appendix S2).

Current-year defoliation, D_t , was measured on the same branches used to estimate egg densities at the end of the season. Twenty-five randomly selected shoots from one branch of each of 10 trees were assigned to one of six damage classes (nil, 1–25%, 26–50%, 51–75%, 76–99%, 100%). Mean D_t for the location was calculated using the midpoint of the damage class of these 250 shoots. Because D_t was usually less than 80% and western spruce budworms rarely feed on previous years' foliage of Douglas-fir, we were able to measure defoliation at least two years previous to the current-year when establishing a sample location. To complete defoliation records for years before direct measurements were available, we regressed the area defoliated in a 5-km diameter area around each location obtained from survey maps of defoliation on observed defoliation. Cumulative defoliation, $\Omega_{n,t}$, over n years previous to year t was calculated from current defoliation (D_t) measured in years $t - n$ to $t - 1$:

$$\Omega_{n,t} = \frac{1}{n} \sum_{k=1}^n D_{t-k}. \quad (1)$$

In subsequent analyses, we use $\Omega_{1,t}$ (defoliation in the previous year) and $\Omega_{5,t}$ (cumulative

defoliation in the previous 5 yr), although $\Omega_{2,t}$ (cumulative defoliation over previous two years) is used to predict shoot density (Appendix S1).

Survival and recruitment rates

Observed density estimates for successive life stages allowed calculation of intra-generation, stage-specific survival rates:

$$h_i = \frac{n_{i+1}}{n_i} \quad (2)$$

where i is the life stage. Thus, egg survival, h_1 , is the proportion of first-instar larvae, n_2 , successfully hatching from eggs, n_1 . Combining survival rates for successive stages creates groupings of particular interest. We focus on h_{2-3} , the rate of survival from first-instar larvae hatching in late summer, n_2 , to successfully established larvae in feeding sites the next spring, n_4 , and h_{4-5} , the rate of survival from established, feeding larvae, n_4 , to emerged adults, n_6 , that is, the feeding and maturation period. Royama et al. (2017) refer to h_{2-3} and h_{4-5} in spruce budworm as the pre-emergence and postemergence intervals, respectively. Generation survival, h_g , is survival from egg, n_1 , to adult, n_6 .

Apparent per-capita fecundity (Régnière and Nealis 2019b), or recruitment rate, h_6 , is the ratio of egg density initiating the next generation, $t + 1$, to moth density in the current generation, t :

$$h_6 = \frac{n_{1,t+1}}{n_{6,t}}. \quad (3)$$

This is equivalent to the E/M (egg to moth) ratio of Royama (1984) and can be compared with an expected recruitment rate calculated from the density of moths in the current generation, $n_{6,t}$, times their expected mean fecundity, F_t , divided by two (assuming a 1:1 female:male ratio). Expected fecundity varies negatively with current-year defoliation, D_t , in spruce budworm and is estimated by $F_t = 216.8 - 1.117D_t$ (Nealis and Régnière 2004b). We verified this relationship for western spruce budworm with two independent measures of expected mean lifetime fecundity of individuals: one for female moths reared as larvae with ample, optimal food (diet; Nealis and Régnière 2014) and a second for moths collected as pupae from source locations where observed defoliation was severe ($D_t = 80\%$). Both measures were very close to mean

fecundities predicted for the given level of defoliation by the regression for spruce budworm, validating this calculation for lifetime fecundity. Realized fecundity in the natal location should be less than expected because of moth mortality. We follow Royama (1984) in approximating expected realized, per-capita fecundity as 0.6 of potential fecundity, F_t .

Intergeneration rates of change, r_i , are the changes in density between generations measured at the same life stage i . We use the egg stage, r_1 :

$$r_1 = \frac{n_{1,t+1}}{n_{1,t}} = h_g h_6. \quad (4)$$

We calculated the variances of all ratios (σ_h and σ_r) from means, variances, and sample sizes (Frishman 1975):

$$\sigma_h \text{ or } \sigma_r = \frac{1}{\mu_i^2} \sqrt{\frac{\mu_i^2 \sigma_j^2}{n_j} + \frac{\mu_j^2 \sigma_i^2}{n_i}} \quad (5)$$

where μ , σ^2 , and n are the mean, variance, and sample size, respectively, of the numerator (i) and denominator (j) of the ratio.

Upper case symbols N_i and H_i represent log-transformations of n_i and h_i , respectively.

Rearing cohorts for natural enemies

Beginning in 2000, all or a subsample up to a maximum of approximately 400 live larvae and pupae from each sample were reared individually on artificial diet (McMorran 1965) in glass vials at 20°C and L:D 16 h:8 h, until either death of the budworm or emergence of a surviving adult. Primary parasitoids that issued from budworm cadavers were recorded as the cause of mortality and identified using available keys (see references in Nealis 2016). Only primary parasitoids directly responsible for the death of budworms are included in calculations (Appendix S3).

Western spruce budworms that died in rearing with no associated parasitoids were examined for micro-pathogens (Nealis et al. 2015). Co-infections occurred but for this analysis, the cause of mortality was assigned on the basis of known pathology for spruce budworm, that is, whenever *ChocNPV* (nucleopolyhedrosis virus) or myco-pathogens were found in cadavers, they were considered the cause of mortality irrespective of other pathogens

present (Lucarotti et al. 2004). Spores of *Nosema* (Microsporidia) are common in live and dead budworms but considered the cause of death only when spore loads in a cadaver were exceptionally high and no other agent found (Eveleigh et al. 2012). Thus, the relative frequencies of pathogens used here are not rates of infection but rates of mortality caused by selected pathogens after excluding budworms killed by parasitoids (Appendix S3). An unknown cause of mortality was assigned to records of larvae and pupae that died but for which the diagnostic protocol did not reveal a specific agent. Overall relative frequency of unknown mortality was <6%, and there was no effect of either location ($F_{7,78} = 0.93$, $P = 0.5$) or year ($F_{1,78} = 2.06$, $P = 0.2$). These were retained in the data set.

Survival rates in reared cohorts were calculated separately for early-season (L_4) and late-season (L_6 and P) cohorts, for each generation at each location. Rearing records were grouped either into the early- or late-season cohort of feeding larvae according to the average instar of the sample cohort (<5 or $\alpha \geq 5$, respectively), and summed. The two most common endoparasitoids, *Apanteles fumiferanae* Vier. (Hymenoptera: Braconidae) and *Glypta fumiferanae* (Vier.) (Hymenoptera: Ichneumonidae), attack neonate budworms in late summer, overwinter within the host larva and kill it the following season. The early-season cohort provides the best estimate of the proportion of the budworm generation killed by these species as all attacks are complete and no parasitoid has exited the host at the time of sampling. As most other parasitoids attacking larvae were just becoming active at the time of the early-season samples, and potential horizontal transmission of pathogens was just beginning (Nealis et al. 2009), rearing mortality from all other natural enemies was estimated using the late-season cohort only. *A. fumiferanae* or *G. fumiferanae* significantly retard development of their hosts and so are also found in late-season cohorts. To avoid double-counting, budworms in late-season cohorts killed by either of these parasitoids were discounted before calculating survival rates from other natural enemies. In this scheme, there is no overlap between species of natural enemies causing mortality.

ANALYSIS

Defoliation and stage-specific survival rates

Annual defoliation, D_t , was related to the log-density of feeding larval stages, N_4 , by:

$$\ln\left(\frac{D_t/100}{1-D_t/100}\right) = p_0 + p_1N_4 + p_2N_4^2 + e \quad (6)$$

where e is an error term. Normality was verified with the Anderson-Darling test (Anderson and Darling 1952).

Stage-specific survival rates (h_{2-3} , h_{4-5}) and the recruitment rate (h_6), estimated with Eqs. 2, 3, respectively, were related to population density at the onset of the life stage (the denominator n_i), current and cumulative defoliation (D_t and $\Omega_{5,t}$), and other variables relevant to a specific life stage, to calculate expected stage-specific survival rates \hat{h}_i .

Because we did not observe infertile eggs, and predation on eggs was rare, survival from egg to neonate larva, h_1 , was the proportion of eggs escaping parasitism by *T. minutum*. This proportion was high overall (average = 0.953 ± 0.011 , SEM, $n = 103$), but varied in an intricate way among locations and years, as well as with egg density. Because of the minor influence of egg parasitism on generation survival, we defer detailed analysis to a future paper.

Survival of neonate larvae from late summer to established, feeding budworms in current-year buds the following spring, h_{2-3} , is the product of survival during dispersal to their hibernacula, S_{d1} , overwinter survival within the hibernaculum, S_o , and survival during dispersal from hibernacula to forage the following spring, S_{d2} , or;

$$h_{2-3} = n_4/n_2 = S_{d1}S_oS_{d2}. \quad (7)$$

To estimate S_o , binomial logistic regression related the overwinter survival data of Nealis and Régnière (2016) from three primary locations (Kirby, Pentangle, and Clapperton) between 1999 and 2015 to various weather-related predictors:

$$S_o = 1/1 + \exp[-(p_0 + p_1E + p_2T_{fall, spring} + p_3T_{minDec-Feb} + p_4Precip_{May} + p_5P(rain)_{May})] \quad (8)$$

where E is elevation, $T_{fall-spring}$ is mean daily temperatures in September and April (when budworms are dormant), $T_{minDec-Feb}$ is mean daily minimum winter temperatures (when budworms are in diapause), $Precip_{May}$ is total precipitation in mm during May, and $P(rain)_{May}$ is the proportion of days in May with precipitation >1 mm (when budworms are emerging from hibernation). BioSIM calculated annual weather statistics for each year and location (Régnière et al. 2014). Eq. 8 was used to calculate S_o for all sites and years.

We used the least angle regression (LAR) method as modified by Efron et al. (2004) to conduct multiple regression analyses of stage-specific survival rates. This stepwise method produces a sequence of regression models by adding an independent variable and calculating associated information criteria (Akaike's information criterion [AIC], Bayesian information criterion [BIC]) at each step. We used leave-one-out cross-validation to calculate the predicted residual sum of squares (PRESS) to select the final model, that is, that which yielded the highest predicted R^2 without being unduly complex (lowest AIC). Least-square parameters for selected independent variables in the final models were estimated using SAS/9.4 Proc GLMSELECT (SAS Institute 2018). Residuals were tested for normality with the Anderson-Darling test.

We related S_{d2} to six potential predictors, using measured dispersal losses P_{loss} in primary locations between 1997 and 2004 (Nealis and Régnière 2009). We defined $S_{d2} = 1 - P_{loss}$ and fitted the model:

$$\ln\left(\frac{S_{d2}}{1-S_{d2}}\right) = p_0 + p_1\Omega_1 + p_2N_2 + p_3\Psi + p_4Precip_{May} + p_5P(rain)_{May} + p_6T_{May} + \epsilon \quad (9)$$

where the predictors tested were as follows: Ω_1 (defoliation in the previous year); N_2 (the log-density of budworms entering the stage); Ψ (foliage weight per ha); $Precip_{May}$ (total precipitation in May); $P(rain)_{May}$ (proportion of days with rain in May); and T_{May} (mean daily temperature in May); and ϵ is an error term. The final form of Eq. 9 was used to calculate S_{d2} for all sites and years.

Estimates of S_o and S_{d2} calculated with Eqs. 8, 9 allowed investigation of various predictors of S_{d1} , the survival of neonate larvae dispersing from the egg mass in search of hibernacula. By rearranging Eq. 7:

$$S_{d1} = n_4 / (n_2 S_o S_{d2}). \quad (10)$$

Note that in the context of the survival interval, h_{2-3} , S_{d1} actually occurs in the calendar-year previous to corresponding S_o and S_{d2} .

Temporal variation of S_{d1} suggests the age of the outbreak in a location may be a significant factor. In the three primary sites in the Okanagan Valley (Fig. 2, red dots), the initial outbreak began in the mid-1980s, and so was older than 10 yr when first sampled in 1998. The outbreak in that area collapsed after 2000 and branch sampling to estimate budworm densities only became practical again once these populations recovered in 2009 (Fig. 3). Elsewhere, the outbreak was just beginning in 1996. A variable, A , representing age of outbreak was created using 1982 as base value for Okanagan locations sampled prior to 2008, and 1996 as base value in all other cases. The value of A was scaled between 0 (youngest) and 1 (oldest). The relationship between S_{d1} and A was strongly curvilinear, so we included an exponent to the age variable, A^n , with the best integer value of n to be determined. We also tested S_{d1} for the effects of elevation (E), defoliation in the previous year (Ω_1 , Ω_1^2), cumulative defoliation in previous 5 yr (Ω_5), foliage weight per ha (Ψ), and density of budworm neonates (N_2) with the model:

$$\ln\left(\frac{S_{d1}}{1 - S_{d1}}\right) = p_0 + p_1 E + p_2 \Omega_1 + p_3 \Omega_1^2 + p_4 \Omega_5 + p_5 \Psi + p_6 N_2 + p_7 A^n + \epsilon \quad (11)$$

where ϵ is an error term. To estimate the best exponent value in term A^n of Eq. 11, n was varied between 1 and 12 (integer values) and Eq. 11 fitted by LAR for each value. The model chosen had the lowest AIC and highest predicted R^2 . Predicted survival of non-feeding larvae, \hat{h}_{2-3} , was then calculated using Eq. 7.

The combined survival of feeding larvae and pupae to emergence as adults, h_{4-5} , was analyzed to identify significant relationships with density

of the budworm population at the beginning of the stage in the previous year ($N_{4,t-1}$), the current-year (N_4) and its square (N_4^2) (these three terms test for lagged and direct density dependence), current defoliation (D), 5-yr cumulative defoliation (Ω_5), age of outbreak as defined above (A^n), and elevation (E):

$$H_{4-5} = p_0 + p_1 N_{4,t-1} + p_2 N_4 + p_3 N_4^2 + p_4 D + p_5 \Omega_5 + p_6 A^n + p_7 E + \epsilon \quad (12)$$

where ϵ is an error term. As above, the best value of exponent n in the age of outbreak term A^n minimized the AIC and maximized predicted R^2 using integer values between 1 and 12. Coefficients of the final model were used to calculate \hat{h}_{4-5} .

Generation survival from egg to adult is the product of component survivals:

$$h_g = h_1 h_{2-3} h_{4-5}. \quad (13)$$

Fractions of the variation in h_g explained by each of its three stage-specific components were calculated (Legendre and Legendre 1998). This analysis calculates the proportion of variation in h_g that is explained by h_{1-3} , holding h_{4-5} constant (fraction [a]), and the proportion explained by h_{4-5} , holding h_{1-3} constant (fraction [c]). The cross-correlation between h_{1-3} and h_{4-5} constitutes fraction [b], a contribution that can be positive or negative, depending on the sign of the covariance. Because of its very small contribution, the variation explained by h_1 was assimilated to the error term (fraction [d]). Given that [a] + [b] + [c] + [d] = 1, these fractions are calculated from the regression R^2 of: $h_g = p_0 + p_1 h_{1-3}$ ($R^2 = [a] + [b]$), $h_g = p_0 + p_1 h_{4-5}$ ($R^2 = [b] + [c]$), and $h_g = p_0 + p_1 h_{2-3} + p_2 h_{4-5}$ ($R^2 = [a] + [b] + [c]$). The remainder, fraction [d] = 1 - ([a] + [b] + [c]).

Egg recruitment

Apparent per-capita recruitment of eggs, h_6 , is the net result of oviposition by local and immigrant moths. Observed annual recruitment rates are compared with expected recruitment rates for evidence of net emigration or immigration. Analysis of these data in the context of general models of migration and recruitment in spruce budworms is presented in Régnière and Nealis

(2019b). Here, we extend the model and present the relationship between per-capita recruitment and local and regional moth densities of western spruce budworm at different elevations with the general linear model:

$$H_6 = p_0 + p_1 N_6 + p_2 \bar{N}_6 + p_3 N_6 \bar{N}_6 + p_4 E + \epsilon \quad (14)$$

where \bar{N}_6 is the log of average adult density among all locations sampled in the regional area in a given year (Fig. 2), E is elevation, and ϵ is an error term. Correlations between ϵ , latitude, and longitude were calculated to check for spatial patterns in the residuals of Eq. 14.

Intergeneration rates of change

Intergeneration rates of change examined change in density of eggs between successive years, $r_1 = n_{1,t+1}/n_{1,t}$, as a function of its two determinant rates: generation survival h_g and recruitment h_6 . The fraction method (Legendre and Legendre 1998) was used to assess relative contributions of these two components of r_1 .

Survival in rearing

Binomial logistic regression related the frequency of specific or groups of natural enemies to log-population density (N) and elevation (E). Elevation was always included as a potential predictor in analyses as it was part of the primary study design and there was evidence of its significance for natural enemies in earlier analyses (Nealis et al. 2009, 2015).

Both *A. fumiferanae* and *G. fumiferanae* are univoltine and considered specialized parasitoids that overwinter in larvae of budworms so there is the possibility their frequency is related to host density in the current and previous generations. Survival from these parasitoids was estimated from early-season cohorts ($\alpha < 5$), and the analysis included $N_2(t-1)$, $N_2(t)$, and E as potential predictors. For all other parasitoids and pathogens, survival was estimated from late-season samples ($\alpha \geq 5$), and the relevant density was $N_4(t)$. The baculovirus, *ChocNPV*, was found in all locations but not in every year. We analyzed the frequency of infection by *ChocNPV* in two stages, first relating the likelihood of the presence of the virus to population density and elevation and then the conditional probability of infection among sites

and years where it was present as a function of these same predictors.

Overall rearing survival S for the generation was the product of survival of larvae from parasitism by *A. fumiferanae* and *G. fumiferanae* in the early samples and survival from other agents in the later samples: $S = S_{AG} \times S_{late}$. The error associated with those survival rates was calculated from the total number of individuals reared as $\sigma_S = \sqrt{S(1-S)/n_{reared}}$. We tested the density dependence of S against the density of feeding larvae $N_4(t)$ by regression analysis.

RESULTS

Defoliation and impacts

The density of Douglas-fir ≥ 10 cm DBH at the primary sample locations ranged from 110 to 610 stems per ha (Table 1). There was no effect of study location on either mean DBH ($F_{7, 218} = 1.64$, $P = 0.12$) or height ($F_{7, 218} = 1.10$, $P = 0.36$) of trees, so differences in foliage biomass among locations reflect differences in the densities of co-dominant trees.

Defoliation (D_t) was closely related to the density of budworms establishing feeding sites in the spring (n_4), increasing from 10% when $n_4 = 4$ larvae per 100 shoots to 90% when $n_4 = 40$. Parameter estimates for Eq. 6 were as follows: $p_0 = -3.804 \pm 0.174$, $p_1 = 0.956 \pm 0.129$, and $p_2 = 0.1874 \pm 0.0372$ ($R^2 = 0.785$). Spruce budworms cause significant damage early in the season despite their small size as they emerge before bud flush and excavate small, developing buds. Competition for food limits the density of adults emerging at the end of the season, giving the diminishing-return shape relationship between n_4 and n_6 , increasing to a maximum of 2 adults/100 shoots as n_4 increases from 10 or 20 L_4 /100 shoots. At that density range, defoliation ranges between 40% and 70%. This relationship is common in many host tree species in budworm systems (Campbell 1993, Nealis and Régnière 2004a).

Annual defoliation exceeded 90% in only 27 of 203 location-years and only once in two consecutive years (2006 and 2007) at two primary locations (Fig. 3a, b). Consequently, mortality of co-dominant trees during this outbreak was low with only three of 27 sample trees dying at one location (Mabel, Table 1) and none elsewhere ($n = 175$). Top-stripping, complete removal of

Table 1. Descriptive statistics for Douglas-fir trees and geographic coordinates for sample locations in the Nicola Valley (Clapperton, Steffens, Kirby, Swakum, Mabel, and Pentangle) and Okanagan Valley (Peachland, Pine Ridge, and Coldham) in British Columbia, Canada.

Location	Coordinates			Stem density (no./ha)	DBH (>10 cm)†		Height (m)†		Foliage (kg/ha)
	°N	°E	Elev.		Initial	2011	Initial	2011	
Nicola									
Clapperton	50.18	-120.67	750	185	26.0 (2.3)‡	28.1 (2.2)	16.3 (1.1)	16.8 (0.1)	4912
Steffens	50.24	-120.82	950	7000	23.0 (1.7)	25.5 (1.8)	15.0 (0.7)	16.1 (0.7)	20,076
Kirby	50.22	-120.65	1050	430	24.2 (1.6)	27.1 (1.8)	13.8 (0.7)	15.0 (0.8)	6614
Swakum	50.13	-120.50	1100	265	24.2 (1.5)	...	11.7 (0.6)	...	8016
Mabel	50.24	-120.61	1135	2340	20.9 (2.2)‡	21.3(2.2)	14.2 (1.0)‡	14.1 (1.0)	14,580
Pentangle	50.24	-120.66	1350	1000	23.2 (1.7)	25.8 (1.9)	14.5 (0.6)	15.8 (0.8)	20,845
Okanagan									
Peachland	49.75	-119.81	600	400	21.2 (1.8)‡	...	15.5 (0.9)‡	...	7064
Pine Ridge	49.77	-119.78	850	468	27.2 (1.8)‡	...	16.4 (0.8)‡	...	8524
Coldham	49.79	-119.79	1050	275	42.7 (2.4)‡	...	14.8 (0.8)‡	...	8061

The absence of measurements is indicated by '...'.
 † Sample sizes range from 21 to 40 trees.
 ‡ Initial measurement in 2004.

foliage from the terminal 1.0 m, was observed infrequently in four of five locations in the Nicola Valley (14 of 122 trees) but all of these recovered by 2016. Mortality is more likely in small size classes of trees (Alfaro et al. 1982), but no census of dead trees <10 cm DBH is available. Mortality of small trees may have occurred in the Okanagan locations where the outbreak began several years before our study commenced. Sampling at locations in the Nicola Valley, however, began within a year or two of initial defoliation yet smaller trees already were more sparse than co-dominant trees (Table 1). Mortality to this size class would not have had a significant impact on local resource availability for western spruce budworm during the outbreak.

Despite repeated defoliation, the DBH and height of co-dominant Douglas-fir increased slightly between 1997 and 2011. The total average gain in radial increment over 14 yr, however, was only 9% and average increase in height only 6% (Table 1). Although tree mortality was low, growth essentially stagnated during the outbreak. Cumulative annual defoliation in the previous two years, Ω_2 , increased the number of buds per kg of host foliage, compensating for loss of foliage in the short term (Appendix S1).

Budworm density

In the Nicola Valley, population densities increased and varied about relatively high mean

densities at all locations after 2000, peaking in 2012 and declining thereafter (Fig. 3a–d). By comparison, budworm populations in the Okanagan Valley had caused measureable defoliation since the mid-1980s (Parfett et al. 1994) and were declining when sampling began in 1998 (Maclauchlan et al. 2018). Our sampling confirmed low budworm densities in the Okanagan Valley between 1998 and 2006 although egg densities stopped declining after 2003. Egg densities rebounded to new maxima in 2010, only to decline again in synchrony with Nicola Valley populations after 2012 (Fig. 3e–g). Despite these phase differences in outbreak chronology of the primary sample locations, there was an overall, highly significant positive relationship between elevation and the average density of eggs initiating a new generation among all sites (log-scale slope: $0.222 \pm 0.042/100$ m; $F_{1, 156} = 28.3$, $P < 0.001$). This gradient represented a 5× increase in egg density (from 14.5 to 76.5 eggs/100 buds) between 600 and 1350 m, the lowest and highest elevations in the study.

Temporal patterns in survival and recruitment

Average survival of small non-feeding budworm larvae, h_{2-3} , was 0.345 ± 0.038 ($n = 51$), five times greater than average survival of feeding larvae and pupae, h_{4-5} , at 0.066 ± 0.006 ($n = 64$; Fig. 4). Temporal patterns in these stage-specific survival rates, and in generation

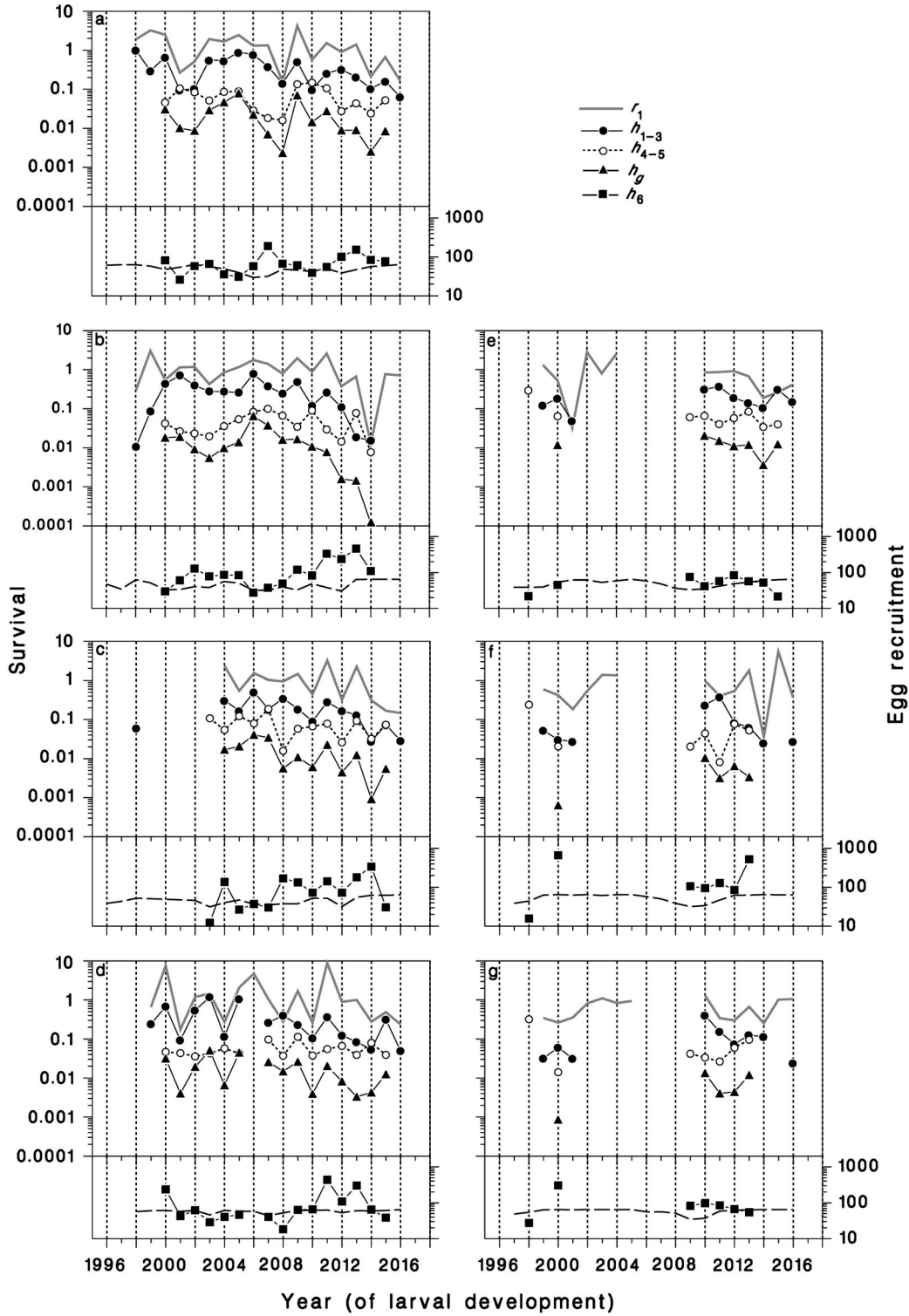


Fig. 4. Observed annual growth rate (r_1 : egg to egg), generation survival (h_g) and its components, early-stage survival (h_{1-3}) and late-stage survival (h_{4-5}), and per-capita recruitment rate (h_6) at seven primary study locations. Locations of panels same as Fig. 3.

survival, h_g , were similar within the major drainages. In the Nicola Valley, h_g varied annually about a relatively high mean level from the beginning of the series until approximately 2005, after which it decreased steadily. This pattern was also evident in h_{2-3} , but not in h_{4-5} at these locations (Fig. 4a–d). Temporal patterns in the Okanagan Valley during this period were more complex as populations collapsed and then recovered. As populations collapsed in the late 1990s, low values of h_g coincided with low values in h_{2-3} , but h_{4-5} did not differ from other years or locations. Following resurgence of populations in 2008, survival rates in these locations resembled those in the Nicola Valley with correlated declining trends in h_{2-3} and h_g , but again, no clear temporal trend in h_{4-5} (Fig. 4e–f).

Per-capita recruitment, h_6 , generally increased over time in the primary sample locations, countering decreasing trends in generation survival (Fig. 4). The long-dashed lines in the lower panels of Fig. 4 represent expected, per-capita realized fecundity as a function of defoliation (see *Survival and recruitment rates*). Before 2008, as populations in the Nicola Valley were increasing, h_6 was near or below this expected rate of recruitment, suggesting neutral or net emigration when populations were increasing. After 2009, observed recruitment rates were greater than expected in most years, indicating net immigration of gravid moths (Fig. 4a–d). This pattern was less obvious in the interrupted Okanagan Valley series as adult densities were too low to measure after 2000, precluding calculation of h_6 . Egg densities recovered after 2002, yet defoliation, and therefore feeding budworm populations, remained relatively low for several more years (Fig. 3e–g). With such low adult densities, h_6 after 2002 must have been high as immigration from the extensive regional outbreak in these years (Fig. 1) contributed to resurgence of Okanagan populations. Observed recruitment in these locations in 2008 and 2009, the first years it could again be calculated, was indeed greater than expected (Fig. 4e–g). Note that recruitment declined in all primary locations in the final year(s) of the outbreak, negating positive changes in generation survival (Fig. 4).

Annual population growth rate

The annual population growth rate at the egg stage, r_1 , is the product of generation survival,

h_g , and per-capita recruitment, h_6 . Generation survival, on its own, explained 91.7% of the variation in r_1 while per-capita recruitment, on its own, explained 53.7%. The sum of these contributions exceeds 100% because of the strong negative correlation between h_g and h_6 (logs, $r = -0.51$, $P < 0.001$). During the latter half of the observation time series, immigration of gravid moths from the large area of high-density populations in BC at that time (Fig. 1) maintained egg recruitment, and therefore r_1 , at greater levels than otherwise would be the case in most locations (Fig. 4). Thus, per-capita apparent fecundity, h_6 , plays a compensatory role in the system via density-related immigration of gravid moths (Régnière and Nealis 2019b).

Natural enemies

Of the 32,694 budworms reared between 2000 and 2016, 10,680 individuals died from one of 18 parasitoid species and 2414 from one of eight pathogen species (Appendix S3). Parasitoids accounted for most mortality and temporal patterns observed in rearing (Fig. 5). Species diversity and rank abundance were remarkably consistent, with all but the least common species (<70 total records) found in all locations in every year. The overwhelmingly dominant parasitoid species, *A. fumiferanae* and *G. fumiferanae*, accounted for 87% of all parasitoids reared from western spruce budworm and a combined rate of parasitism of 0.31 in the early-season cohort ($n = 18,015$). The rate of mortality by these two parasitoids increased with host density at the beginning of the susceptible stage, $N_2(t)$, but was independent of elevation, E (Table 2).

The combined rate of parasitism by all other parasitoid species was only 0.036 ($n = 5976$). This rate also was related positively to the density of budworms entering the susceptible stage, N_4 , and decreased at higher elevations, E (Table 2). Compared to *A. fumiferanae* and *G. fumiferanae*, the combined impact of these parasitoids from late-season cohorts was less consistent among years and locations (Fig. 5, note the difference between rates by *Apanteles* and *Glypta* combined and all parasitoids). Consequently, apparent increases in total mortality were often the result of increases in rates by this group of parasitoid species (e.g., Fig. 5a 2012–2015; Fig. 5b, c 2006; Fig. 5d 2005).

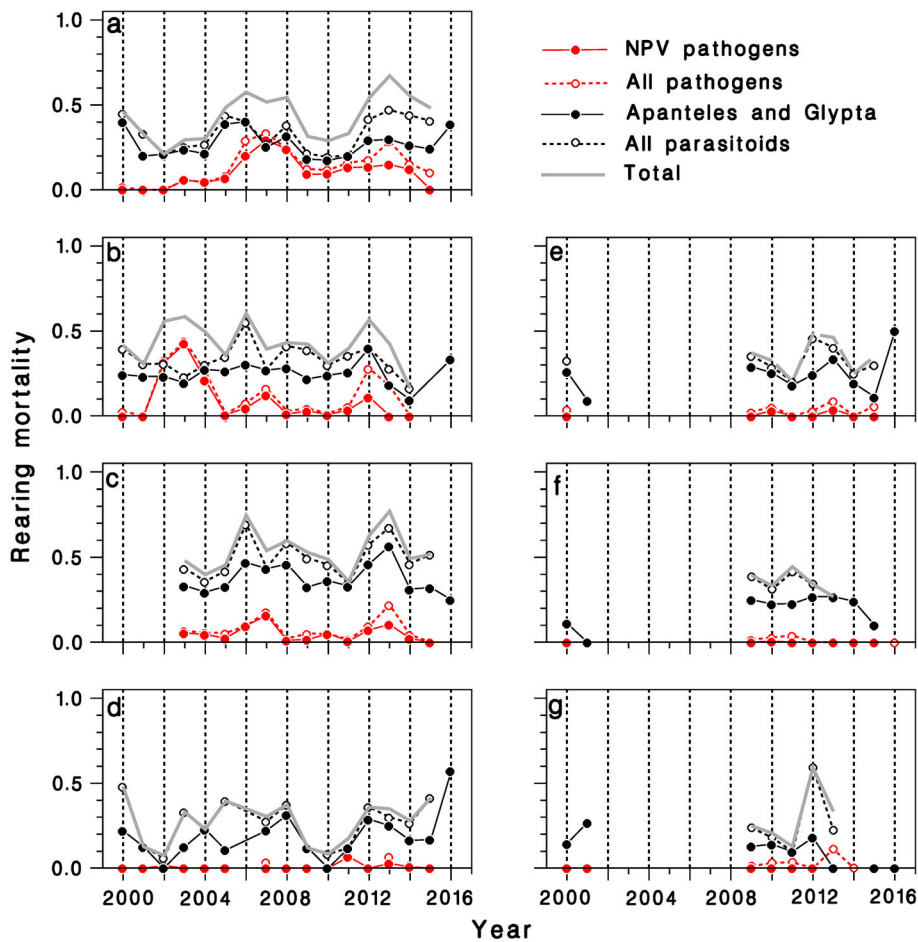


Fig. 5. Rearing mortality by parasitoids and pathogens in cohorts of western spruce budworm at primary locations, 2000–2015. Locations of panels same as Fig. 3.

Table 2. Binary logistic regression of counts of species and groups of natural enemies (parasitoids and pathogens), causing mortality in reared cohorts of western spruce budworm in study locations between 2000 and 2016.

Group	Term	Value	SE	χ^2	P	Odds ratio	95% CI
<i>Apanteles</i> and <i>Glypta</i>	$N_2(t)$	0.2159	0.0279	59.83	<0.001	1.175	1.311
Other parasitoids	N_4	0.1302	0.0507	6.6	0.01	1.031	1.258
	E (/100 m)	-0.0698	0.0507	14.7	<0.001	0.900	0.967
<i>ChocNPV</i>	N_4	0.967	0.247	15.44	<0.001	1.624	4.258
	Presence	E (/100 m)	0.391	0.119	10.84	0.001	1.172
Frequency	E (/100 m)	0.1851	0.0253	53.46	<0.001	1.145	1.265
Other pathogens	E (/100 m)	-0.2184	0.0378	33.46	<0.001	1.155	1.340

Notes: CI, confidence interval; SE, standard error. Intercepts not shown.

The baculovirus *ChocNPV* accounted for 73% of all pathogen-caused mortality. It was ubiquitous but its impact episodic, increasing quickly at very high densities in some locations and

returning to low background levels as soon as budworm densities declined. The likelihood of its presence in a location was positively and strongly dependent on the density of budworms

entering the feeding stage, N_4 . Both the probability of its presence and its relative frequency increased at higher elevations (Table 2, Fig. 5a, b). The combined frequency of all other pathogens was density-independent and decreased with elevation (Table 2).

Stage-specific survival

As indicated by Eq. 7, survival of non-feeding budworm, h_{2-3} , is the combined result of dispersal losses when L_1 search for hibernacula, overwinter survival of L_2 , and dispersal losses the following spring as L_{2-3} forage for feeding sites. Overwinter survival, S_o (Eq. 8), was related positively to elevation, E ($p_1 = 0.148 \pm 0.009/100$ m, $\chi^2 = 247.0$, $P < 0.001$), minimum temperature in the winter months during diapause ($p_3 = 0.355 \pm 0.015$, $\chi^2 = 577.5$, $P < 0.001$), and the proportion of rainy days during the emergence period in May ($p_5 = 4.64 \pm 0.28$, $\chi^2 = 273.4$, $P < 0.001$). It was negatively related to warmer fall and spring temperatures during the dormant period ($p_2 = -0.336 \pm 0.017$, $\chi^2 = 429.6$, $P < 0.001$) and total precipitation in May ($p_4 = -0.054 \pm 0.002$, $\chi^2 = 472.6$, $P < 0.001$). Total precipitation and proportion of days with rain in May were highly correlated ($r = 0.81$), yet these variables had opposite effects on S_o . Overwinter survival was greatest overall between 2003 and 2009, a temporal pattern caused by the combined variation of weather variables shared by nearby locations, modified by their respective elevations (Fig. 6). These results confirm that relatively warm conditions reduce overwinter survival of western spruce budworm while cooler temperatures are conserving (Nealis and Régnière 2016).

The best predictive model of survival of budworms dispersing from their hibernacula to their feeding sites in current-year buds, S_{d2} , included all predictors of Eq. 9 except the amount of precipitation in May ($\text{Precip}_{\text{May}}$; Table 3). S_{d2} decreased with defoliation in the previous year Ω_1 and very slightly with population density N_2 , but increased with greater foliage biomass, Ψ , warmer temperatures in May, T_{May} and higher proportion of rainy days in May, $P(\text{rain})_{\text{May}}$ (Table 3). Local conditions reflecting the structural attributes of the habitat significant to foraging, foliage density modified by defoliation, affect survival during this dispersal event. A denser foliage canopy at

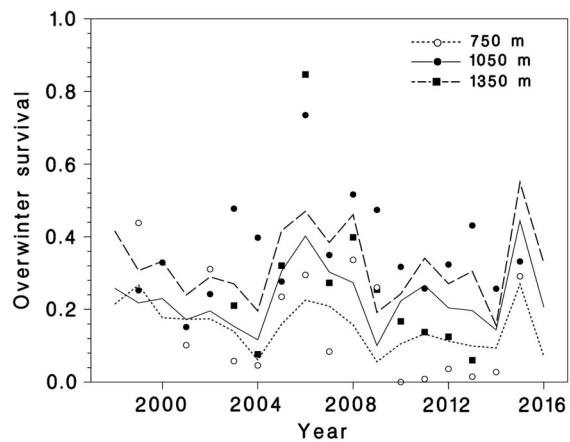


Fig. 6. Observed and predicted overwinter survival, S_o , from 1998 to 2016 in Clapperton (750 m), Kirby (1050 m), and Pentangle (1350 m) as measured with insects overwintered on host trees (Nealis and Régnière 2016). Lines: Eq. 8.

both the tree and stand levels lowers the risk of dispersal. Warm spring conditions favor successful emergence and subsequent foraging, and occasional rain would conserve those budworms still in their hibernacula during this protracted event (Nealis and Régnière 2009).

The best set of predictors of survival of neonate budworms dispersing to their hibernation sites, S_{d1} (Eq. 11), included all terms except cumulative defoliation Ω_5 (Table 3, Fig. 7a). There was a strong curvilinear decrease in S_{d1} with the age of outbreak A^n , with the exponent $n = 8$ yielding the lowest AIC and predicted R^2 (Fig. 7b). Survival in this life stage also decreased sharply at greater densities of neonates, n_2 (Fig. 7c), and with increasing foliage biomass in the stand Ψ (Fig. 7d). Survival increased asymptotically with previous year defoliation, Ω_{1t} , to a maximum near 60% defoliation (Fig. 7e). An important caveat is the absolute values of these estimates for S_{d1} tended to be >1.0 because our method results in S_{d1} accommodating any underestimation of the two other components of h_{2-3} (S_o and S_{d2}), as well as redistribution of budworms within the host crown during the two dispersal events. Nonetheless, the analysis provides insight into the relative importance of factors affecting survival during dispersal from the egg mass to overwintering sites. Increased losses at greater densities of neonates may have been the

Table 3. Parameters and fit statistics obtained by LAR regression (Eqs. 9, 11, 12) for stage-specific survivals: S_{d2} , survival of small larvae (L_{2-3}) foraging in spring; S_{d1} , survival of neonates (L_1) seeking hibernation sites in late summer; H_{4-5} , log survival of feeding larvae (L_{4-6}).

Terms	AIC	Fit statistics			Least-squares estimates	
		BIC	Adj. R^2	Pred. R^2	Value	SE
S_{d2} , Eq. 9, intercept: -4.194 ± 1.497						
Ψ	8.60	-10.47	0.45	0.43	0.105	0.020
N_2	5.61	-12.87	0.56	0.52	-0.003	0.207
T_{May}	5.00	-12.83	0.60	0.52	0.301	0.087
Ω_1	5.02	-11.88	0.61	0.47	-0.012	0.006
$P_{RainMay}$	-1.39	-11.38	0.74	0.61	6.940	2.617
$Precip_{May}$	0.16	-8.02	0.72	0.56		
S_{d1} , Eq. 11, intercept: 2.745 ± 0.444						
A^{10}	95.184	-16.226	0.299	0.296	-13.849	1.801
Ψ	82.726	-28.611	0.380	0.372	-0.059	0.015
N_2	62.492	-47.758	0.488	0.472	-0.633	0.110
Ω_1	60.840	-49.143	0.500	0.478	0.032	0.011
E	61.425	-48.398	0.502	0.477	0.0005	0.0005
Ω_1^2	57.479	-51.536	0.524	0.495	-0.0002	0.0001
Ω_5	58.729	-50.028	0.522	0.485		
H_{4-5} , Eq. 12, intercept: -3.157 ± 0.327						
A^7	9.727	-78.394	0.027	0.016	-1.351	0.521
N_4^2	7.485	-80.407	0.062	0.043	-0.049	0.018
E	5.728	-81.779	0.091	0.062	0.0006	0.0003
$N_{4,t-1}$	7.454	-79.896	0.083	0.049		
Ω_5	9.173	-78.005	0.074	0.018		
N_4	8.726	-77.902	0.089	0.017		
D	10.680	-75.740	0.078	0.001		

Notes: AIC, Akaike's information criterion; BIC, bayesian information criterion; LAR, least angle regression; SE, standard error. Best value of fit statistics is bolded. Final models chosen using the minimum predicted (cross-validation) R^2 .

result of increased movement as budworms competed for the most protected hibernation sites (Nealis and Régnière 2016).

The stand-level influence of previous defoliation and foliage biomass on S_{d1} was contrary to the effect of these same factors on survival of budworms when dispersing from their hibernacula to forage the following spring S_{d2} (Table 3). This apparent contradiction may result from the distinct behavior of small budworms during each of these dispersal events. Neonates disperse in late summer, seeking protected niches on woody surfaces in the interior of the tree (Nealis and Régnière 2016). At that time, foliage is simply more substrate to traverse while seeking suitable hibernation sites. If dislodged during dispersal, convective air movement typical of summer would displace them downwards, still within the canopy. By comparison, spring dispersing budworms are photopositive, foraging for suitable foliage at the branch tips and often ballooning

between trees in unstable spring weather conditions (Wellington and Henson 1947). Greater foliage density has a positive effect on survival as losses are greatest in stands with fewer co-dominant trees and a sparse understory (Régnière and Fletcher 1983, Nealis and Régnière 2009). Losses in all stands increase as a result of defoliation which increases the likelihood of budworms ballooning between trees in the foraging process. Hence, the compensatory nature of tree and stand condition on sequential survival rates during the non-feeding larval stages.

Expected values for overall survival during the small non-feeding larval period, h_{2-3} , (Eq. 7) were highly correlated with observations ($r = 0.692$; Fig. 8b) as were yearly averages of observed and predicted h_{2-3} ($r = 0.75$; Fig. 8a). Many of the low values for h_{2-3} during the late 1990s and early 2000s were associated with low S_{d1} survival in the Okanagan Valley (red points in Fig. 8a) where the prolonged outbreak had already affected the

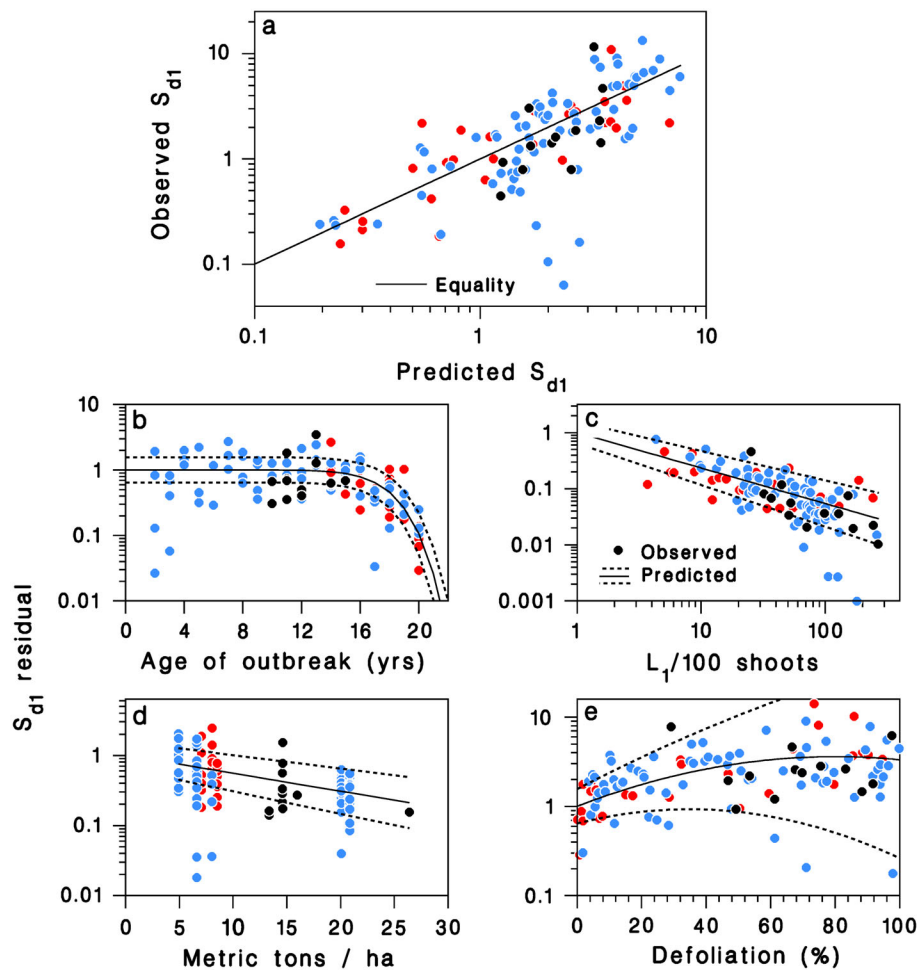


Fig. 7. Survival of dispersing neonate budworm, S_{d1} , (a) observed versus predicted S_{d1} . (b–e) Residual effects of (b) age of outbreak A , in years; (c) density of neonates, n_2 ; (d) foliage weight, Ψ ; (e) defoliation caused by previous generation of feeding larvae Ω_1 (solid lines, Eq. 11; dotted lines, \pm standard error of corresponding coefficients). Colors refer to plot locations (and outbreak history), as per Fig. 2 (red, Okanagan Valley; blue, Nicola Valley; black, everywhere else).

forest resource negatively (Fig. 7a). Overall, h_{2-3} in the Nicola Valley increased early in the outbreak and remained high until 2007, enhanced by a brief period of improved overwinter survival (Fig. 6). Survival of these early-larval stages then decreased steadily for the remainder of the outbreak as population densities and defoliation increased (Fig. 3). These events affected survival of budworms negatively during larval dispersal, a direct and immediate effect during dispersal of neonates in late summer (Fig. 7) and an indirect and lagged effect via the influence of previous defoliation on survival during dispersal the next

spring (Table 3). Despite eventual decline in budworm densities and defoliation associated with these changes in survival, h_{2-3} continued to decrease (Fig. 8a) as survival of neonates declined with the negative effects of prolonged outbreaks on stand condition (Fig. 7b) and the unfavorable change in overwinter survival in the same period (Fig. 6). These effects were exacerbated by the cumulative, negative effects of persistent defoliation on survival of foraging budworms during dispersal the following spring.

By comparison, survival of feeding larvae and pupae, h_{4-5} , exhibited no temporal trend and varied

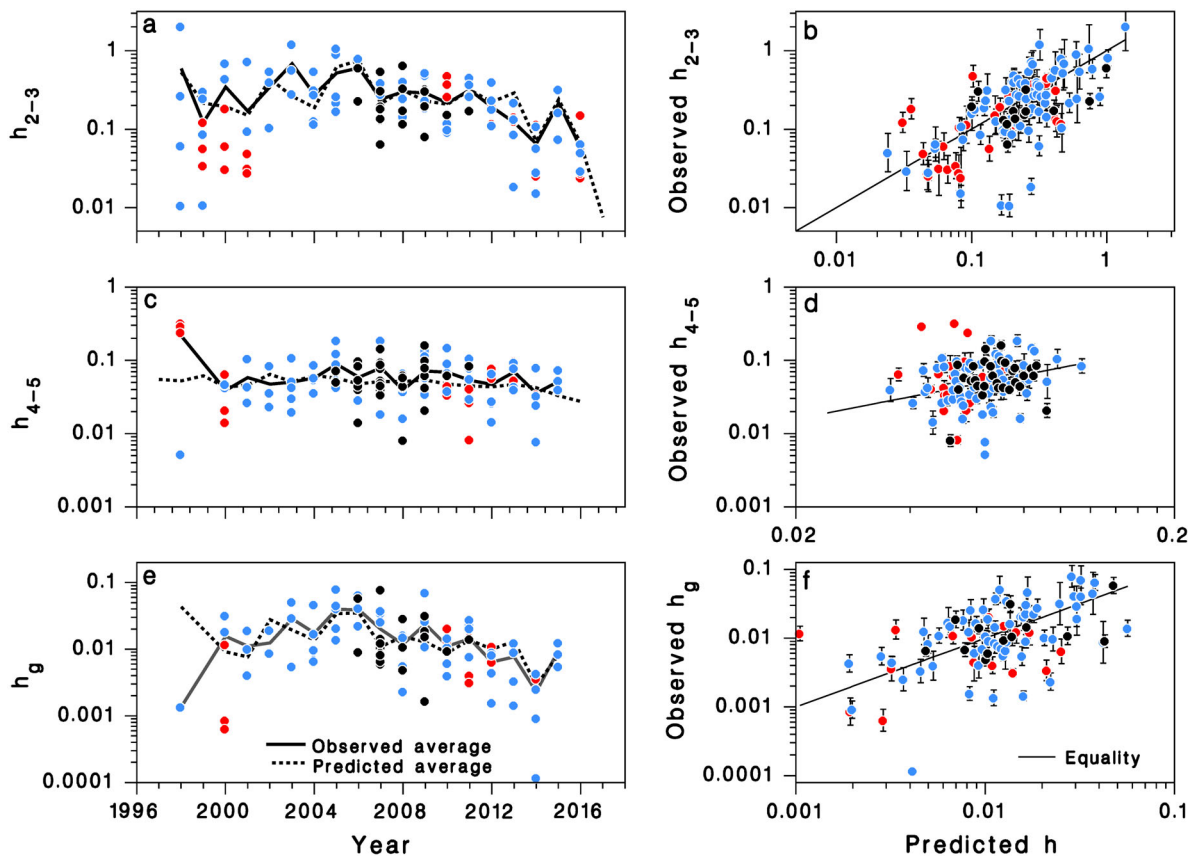


Fig. 8. Survival of western spruce budworm during (a, b) the early-larval stages (h_{2-3}), (c, d) late-larval and pupal stages (h_{4-5}), and (e, f) their combination into generation survival h_g . (a, c, e) Time trends, with observed average (solid lines) and predicted average (dotted lines). Symbol colors refer to plot locations (and outbreak history), as per Fig. 2 (red, Okanagan Valley; blue, Nicola Valley; black, everywhere else). (b, d, f) Observed values against values predicted by Eqs. 7, 12, 13, respectively. Solid lines: equality.

substantially among locations in any one year (Fig. 8c). While Eq. 12 provided some predictive explanation of this variation, both adjusted R^2 and predicted R^2 were low (Table 3). Nevertheless, survival during this life stage also decreased with outbreak age A , dipping sharply in outbreaks >15 yr old (Fig. 9a). The best-fitting exponent, based on the AIC and cross-validation R^2 , was A^7 . Survival during this stage also decreased with budworm density entering the stage, n_4 , especially at densities greater than 5–10 $L_4/100$ shoots (Fig. 9b).

A relationship between rearing survival, S , and density, n_4 ($F = 16.0$, $df = 1, 108$, $P < 0.001$) corresponds closely to the decreases in h_{4-5} at higher densities (Fig. 9c). We expected survival in rearing to also decline at lower budworm densities as observed in spruce budworm (Régnière

and Nealis 2007, Royama et al. 2017). Our data, however, were not sufficient to detect such a pattern, if it does exist, because data from very low-density populations are sparse and cohort sizes small. It is possible density-related mortality factors other than parasitoids or pathogens operate in the relatively low-density western spruce budworm populations observed in this study (see *Discussion*).

Generation survival, h_g , is the product of survival in all successive stages and is predicted by Eq. 13 ($r = 0.549$, $P < 0.001$; Fig. 8e). Partition of variance (Legendre and Legendre 1998) indicates h_{2-3} and h_{4-5} together account for 98.7% of the variance of h_g (56.4% for h_{2-3} , 35.8% for h_{4-5} , and 6.5% due to their cross-correlation), with the remaining 1.3% resulting from h_1 . While survival

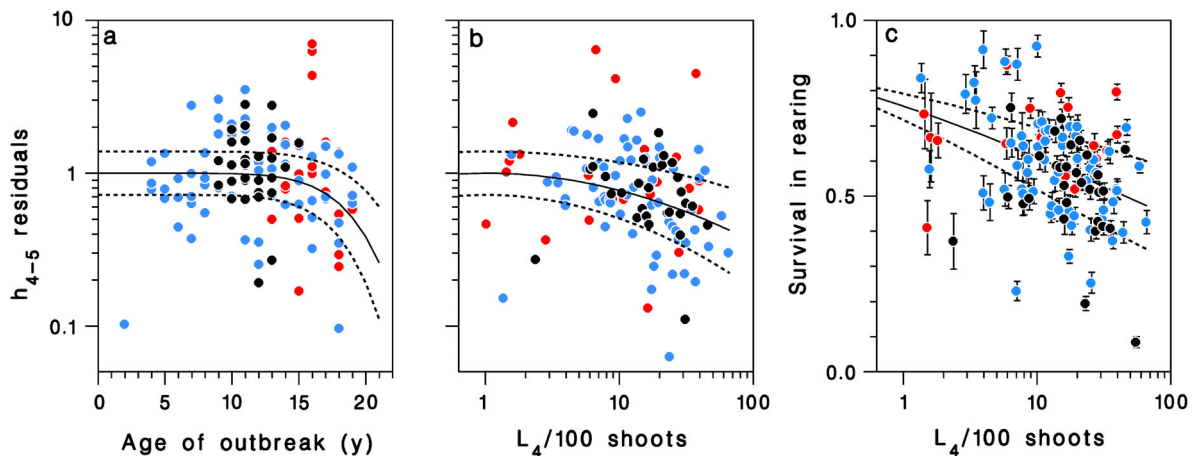


Fig. 9. Factors affecting survival of western spruce budworm feeding larvae and pupae, h_{4-5} . (a) Effect of age of outbreak and (b) effect of population density. (c) Density dependence of survival in rearing. Colors refer to plot locations (and outbreak history), as per Fig. 2 (red, Okanagan Valley; blue, Nicola Valley; black, everywhere else).

of non-feeding larvae h_{2-3} (Fig. 8a) accounted for much of the temporal pattern of h_g (Fig. 8e), the magnitude of h_g was influenced greatly by h_{4-5} (0.066 ± 0.005 , mean \pm standard error), which was much lower than h_{2-3} (0.332 ± 0.031). There were strong compensatory relationships between survival within a generation and budworm density throughout the life history. Survival of non-feeding larval stages, h_{2-3} , decreased monotonically with the density of larvae entering the stage through the negative effect of neonate density, n_1 , on S_{d1} (Fig. 7b), but survival of feeding larvae and pupae, h_{4-5} , had a parabolic relationship with density of larvae entering the stage (Fig. 9 b). The net effect was a significant, negative relationship between density of budworm initiating the generation, n_1 , and generation survival, h_g (Slope -0.452 ± 0.141 m; $F_{1,95} = 10.4$, $P = 0.002$), and a significant positive relationship with elevation of the location ($0.174 \pm 0.054/100$ m, $F_{1,95} = 7.5$; $P = 0.007$).

Egg recruitment and moth dispersal

Spatial and temporal fluctuations in the recruitment rate, h_6 , indicate the intensity of moth migration at the regional level and the significance of net migration to recruitment of eggs at the local level (Régnière and Nealis 2019b). If moths did not disperse, or if emigration and immigration of gravid females balanced exactly in all locations,

the recruitment rate, h_6 , would be equal to expected, realized per-capita fecundity, \hat{F}_t . In this case, there would be no relationship between local adult density, n_6 , and the recruitment rate (Fig. 10 a, horizontal dotted line). At the other extreme, where all moths disperse and there is total mixing of eggs at the regional scale, the relationship between h_6 and n_6 would have a maximum slope (-1 ; Fig. 10a, diagonal dotted line). In fact, there was an overall negative relationship between the recruitment rate, H_6 , and local adult density, N_6 (Fig. 10a, solid diagonal line; slope -0.448 ± 0.058 ; $F_{1,112} = 58.61$, $P < 0.001$, $R^2 = 0.344$), indicating considerable net migration of gravid female moths from high- to low-density populations. The significant interaction between local and regional moth densities (Table 3) reflects the density-dependent nature of net recruitment (Régnière and Nealis 2019b). Our data and Eq. 14 show no detectable net migration when local and regional moth densities were equal ($n_6/\bar{n}_6 = 1$; dotted lines in Fig. 10b). Net immigration occurs in populations that are significantly lower than the regional average, and conversely, net emigration occurs in populations where density is significantly higher than the average (see also Campbell et al. 1983a). There was also a slight but significant increase in H_6 with elevation E ($0.063 \pm 0.031/100$ m, $F_{1,109} = 4.17$, $P = 0.044$) commensurate with significantly greater egg

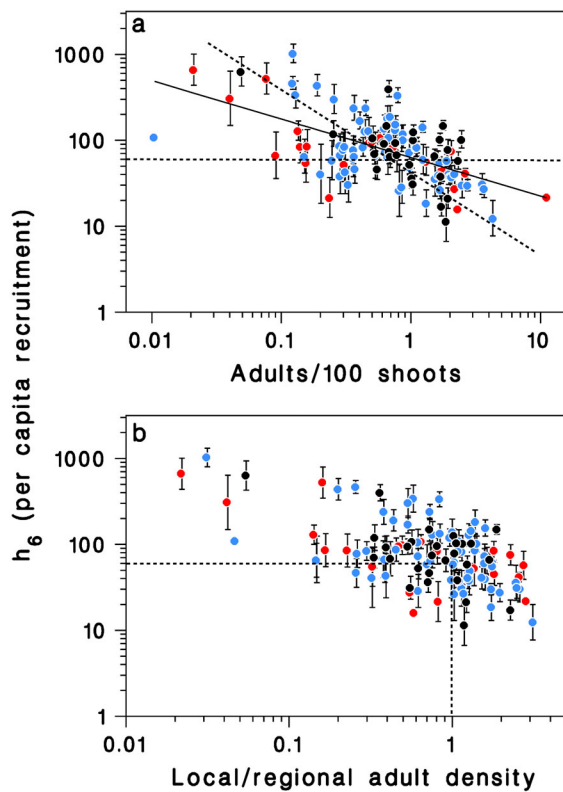


Fig. 10. (a) Observed h_6 or per-capita recruitment rate (\pm standard error) as function of local adult density. Solid line: regression. Horizontal dotted line: expected maximum realized per-capita fecundity. Diagonal dotted line: line of maximum slope (-1) under total mixing of eggs at regional scale by migration. (b) h_6 relative to ratio between local and regional moth densities (n_6/\bar{n}_6). No net immigration occurs when local and regional adult densities are the same ($n_6/\bar{n}_6 = 1$, dotted lines). Colors refer to plot locations (and outbreak history), as per Fig. 2 (red, Okanagan Valley; blue, Nicola Valley; black, everywhere else).

densities at higher elevations mentioned earlier. This model explains 63.2% of the variation of h_6 in our data set. There was no correlation between residuals of Eq. 14, latitude ($r = 0.012$, 95% confidence interval [CI] = $-0.172, 0.196$), or longitude ($r = -0.022$, 95% CI = $-0.205, 0.163$), indicating that observed patterns were independent of geographic location. The density-dependent dispersal process of gravid moths over the entire region of Fig. 2 accounts for most of the observed patterns in synchrony and maintenance of outbreak populations of western spruce budworm.

DISCUSSION

Periodic irruptions of animal populations hold a central interest in ecology. Elton (1924) defined the theoretical basis for modern population ecology, relating fluctuations in animal numbers to ecological relationships in a community's trophic structure. His enduring empirical legacy was establishing the importance of systematic population surveys combined with field studies to examine mechanisms of population change. These methods have been the source of the rich information on outbreaks of forest defoliators in North America.

Perspectives on the population dynamics of conifer-feeding budworms originate from experience with the spruce budworm, *C. fumiferana*. Other closely related budworm species which outbreak in different forest ecozones offer an opportunity for comparative studies based on similar sampling and analytic methods (Nealis 2016). This study combines replicated time series of population change and stage-specific survival of western spruce budworm, *C. occidentalis*, with field studies of ecological processes influencing fluctuations in densities during an outbreak. In western spruce budworm, we see the same low-frequency, variable-duration outbreaks as in spruce budworm, as well as similar drivers of dynamics. Defoliation and resulting impacts are constrained by negative feedbacks from density-related processes and substantial mortality from a natural enemy fauna that is remarkably similar among all conifer-feeding budworms. This suite of natural enemies has been implicated as the cause of population collapse (Royama 1984, Régnière and Nealis 2007, Royama et al. 2017), or at least the ultimate agents in the cumulative interaction of trophic relationships that bring about the same end (Régnière and Nealis 2008, Nealis 2016, Cooke et al. 2020). Our study also shows that in western spruce budworm, factors other than natural enemies play important roles in population cycles and that diverse, density-related interactions among trophic levels can prolong and synchronize outbreaks over large forest regions. The ecological relationships revealed in western spruce budworm are also at play in other conifer-feeding spruce budworms. They vary in their strength and apparent impact among different budworm species as a result of associated

relationships with respective hosts (Nealis 2016). Nonetheless, these trophic interactions affect population behavior because of their characteristic sequence in the life cycle of budworms.

Generation survival (egg to adult) of western spruce budworm was largely a function of local processes and varied greatly within and among populations during the early years of the outbreak. Nonetheless, populations peaked at primary study locations within a year of each other and then coalesced into gradual, multigenerational declines in generation survival for the duration of the outbreak. Despite this prolonged period of defoliation, mortality of co-dominant trees in our study locations was low. Negative feedbacks resulting from damage to the host do play a role in population dynamics but starvation resulting from catastrophic loss of resource is infrequent. Moreover, the significant, systemic negative effects of host damage on budworm survival occur earlier in the life cycle, in the non-feeding stages. These effects are evident as gradual but sustained decreases in survival of the early-larval stages (h_{2-3}), sometimes amplified later in the life cycle by increases in mortality by natural enemies, and sometimes moderated at the end of the life cycle by net recruitment of eggs via moths dispersing from areas of higher population densities.

Survival of small western spruce budworm larvae (h_{2-3}) was consistently greater than that of feeding larvae and pupae (h_{4-5}), whereas there was no difference in survival rates of these stages in spruce budworm (Royama 1984, Régnière and Nealis 2007, Royama et al. 2017). This resulted in temporal trends in survival of non-feeding western spruce budworm correlated significantly with trends in generation survival whereas generation survival of spruce budworm was influenced more by survival of later stages (Royama 1984, Régnière and Nealis 2007, Royama et al. 2017). This difference between the two budworms may be related, in part, to study design. Morris (1963b) concluded survival of early-stage larvae was an important source of spatial variation in populations and survival of feeding larvae more influential on temporal rates of change. Consequently, weak relationships between generation survival and early-stage survival were found in spruce budworm studies with relatively few (Royama 1984, Royama et al. 2017) or spatially disjunct (Régnière and Nealis 2007) study locations. This

study, and that of Campbell (1993), analyzed western spruce budworm data from many populations within a region and found evidence of a significant influence of small-larval survival on population rates of change.

Survival of small western spruce budworm larvae was greatest early in the outbreak but soon decreased, primarily as a result of increasing dispersal losses of neonates in late summer and of larvae while foraging the following spring. For neonates, the negative effects of high population densities and sustained defoliation over time on survival are significant. For spring dispersing larvae, however, there is an immediate negative effect of previous defoliation on survival, especially in sparse forest stands (Nealis and Régnière 2009). The more foliage, the more likely budworms find suitable needle clusters to mine and can exploit a wider range of bud flush phenology in the spring (Nealis and Nault 2005). The significance of spatially explicit, stand-level factors such as local foliage biomass, modified by damage-related changes in forest condition, indicates a close association between survival of small budworm larvae and spatial variation in dynamics of western spruce budworm (Campbell 1993).

Between these two dispersal events, overwintering survival of early-stage western spruce budworms was related primarily to weather. Warm temperatures during the dormant periods before (fall) and after (spring) physiological diapause deplete the finite reserves of small budworms more rapidly, causing significant mortality (Nealis and Régnière 2016). Collapse of previous outbreaks of western spruce budworm followed extremely warm weather during moth flight (Thomson et al. 1984), that is, early in the neonatal period before diapause. Such dramatic, immediate effects of winter weather are more likely observed at the bioclimatic margins of current ranges, but, if sustained, will affect long-term population behavior (Régnière and Nealis 2019a). Historical defoliation records from BC indicate a clear shift from repeated outbreaks in low-elevation areas where late summer temperatures have become warmer, to the contemporary, sustained outbreaks on the cooler plateaus of the BC interior (Maclauchlan et al. 2018).

Once emerged, warm, dry weather favors feeding budworms (Wellington et al. 1950,

Thomson et al. 1984). Why this is so is uncertain (Royama 1984). We propose that increases in budworm densities following a series of warm, dry spring conditions are the result of improved survival of feeding stages associated with several weather-related processes. Warm, dry weather promotes production of pollen cones in conifers which serve as a nutritional bridge between the precocious emergence of budworms in the spring and availability of current-year buds (Nealis 2016, Bouchard et al. 2017) and enables early emergence and rapid dispersal to available feeding sites (Nealis and Régnière 2009). These same weather conditions ensure a greater likelihood of maturing within a favorable phenological window when current-year foliage is most nutritious, and avoiding late-season frost mortality, thereby improving fitness overall (Nealis 2012, Régnière and Nealis 2018, 2019a).

White (2018) proposed an alternative hypothesis of why dry, warm weather favors spruce budworm outbreaks. He argued all herbivores are limited by nitrogen availability. Outbreaks are triggered by temporary improvement in the adequacy of plant quality, often associated with drought which accelerates senescence of foliage, releasing soluble amino acids. In the case of spruce budworms, the benefits of this change accrue to small larvae which feed first on senescing older foliage and then switch to nutritious, fresh growth as buds flush. The positive effects of this change in nutritional quality on population growth would be most apparent in the years of transition from low to high densities where, unfortunately, there is a paucity of population data to test White's hypothesis. However, the plant-stress hypothesis is consistent with several independent observations on conifer-feeding budworms (Nealis 2019). The association between postemergence survival of budworm and weather at the local scale and climate-related range shifts in the location of outbreaks at the large scale (Régnière and Nealis 2019a) are evidence, as is the historical association of defoliation with relatively dry sites and arid climatic conditions (Maclauchlan et al. 2006, 2018).

Survival of feeding western spruce budworm increased with increasing densities up to 10 L₄/100 buds and then decreased at greater densities, as in spruce budworm (Régnière and Nealis 2007). Decreases in survival at the greatest

densities were correlated with increases in rates of attack on the feeding stages by diverse parasitoids and, in western spruce budworm, infections of a baculovirus, *ChocNPV*. Such clear, episodic influence of a pathogen is unknown in spruce budworm (Lucarotti et al. 2004). In fact, a cryptic, virulent pathogen hypothesized as responsible for collapses of spruce budworm populations by Royama (1984) was not found in a recent, exhaustive search (Royama et al. 2017). Notable as the widespread occurrences of fatal *ChocNPV* infections were in western spruce budworm, they served only to limit survival at the greatest host densities, quickly reducing populations to less extreme densities. In the eastern spruce budworm, some pathogenic fungi play a similar role but observed epizootics appear more localized (Perry and Régnière 1986).

At the lowest densities of western spruce budworm, small sample sizes in reared cohorts provided insufficient evidence for an important role for natural enemies in the observed decline of survival at lower densities. Experimental studies indicate predation by birds and ants are important at lower densities of western spruce budworm (Campbell et al. 1983b, Torgersen et al. 1984). Royama et al. (2017) deduced specialized forest birds accounted for the disappearance of spruce budworms at these lower densities. It is possible that a variety of predators with differing functional responses at different budworm densities are potentially available to attack budworms in different forest types.

Parasitoids reared from field-collected conifer-feeding budworms provide the most complete, direct measures of the impact of natural enemies. The general features of parasitoid impacts are common to nearly all field studies. The parasitoids, *A. fumiferanae* and *G. fumiferanae*, inflict the greatest mortality in all years and locations, by far. But their relative frequency tracks the moderate changes in western spruce budworm density during the outbreak, and so their impact is relatively constant from year to year at all locations. Consequently, even slight increases in mortality caused by natural enemies later in the life cycle can cause a significant increase in overall mortality, particularly if factors acting earlier have reduced budworm to critical densities (Royama et al. 2017). Unless these increases in natural enemies occur when generation survival and

budworm densities are already declining because of the combined effects of other factors, their effect will also be temporary and populations can rebound (Fig. 5; Nealis et al. 2015).

Published studies on all major *Choristoneura* consistently claim a relationship between rapid collapse of populations at the end of an outbreak with increases in attacks by particular parasitoids including *Meteorus trachynotus* Vier. (Hymenoptera: Braconidae), *Actia interrupta* Curran (Diptera: Tachinidae), and *Lypha setifacies* Brookes (Diptera: Tachinidae) (Régnière and Nealis 2007, Nealis 2016, Royama et al. 2017). In western spruce budworm, these parasitoids, as well as *Phytodietus fumiferanae* Rowher (Hymenoptera: Ichneumonidae) and *Ceromasia auricaudata* Townsend (Diptera: Tachinidae), have a similar relationship to phase of outbreak (Wilkes et al. 1948, Carolin and Coulter 1959, McKnight 1974). All of these species were present in western spruce budworm populations in this study, but were conspicuously uncommon throughout (Appendix S3). Yet budworm populations collapsed nonetheless.

A recent interpretation from field studies of spruce budworm proposes the entire parasitoid complex is dynamically ordered through interactions with other species, and so behaves as an organized unit (Royama et al. 2017). Thus, the infrequent occurrence of particular parasitoids otherwise common and associated with population declines of budworms in other locations and years is significant in our study. An hypothesis suggested by B.J. Cooke is the historical absence of western spruce budworm outbreaks at our study locations has resulted in enemy-free space. High-density populations of western spruce budworm are novel, and the resident populations of alternative hosts necessary to support populations of generalist parasitoids impoverished. A related explanation is that not all species of natural enemies have the climatic tolerance to occupy the recently expanded range of the western spruce budworm as a result of greater recruitment and survival rates at higher elevations. Evidence for this is that the two dominant parasitoids, *Apanteles* and *Glypta*, and the only significant pathogen species, *ChocNPV*, also had greater relative frequencies at higher elevations while the impact of less common species associated with the collapse of outbreaks actually decreased with elevation (Table 2).

The sequence of stage-specific survival rates combined to produce a simple numerical relationship between generation survival and density of western spruce budworm. At low budworm densities, high survival of non-feeding larvae mitigated low survival of later stages. At intermediate outbreak densities, survival of non-feeding stages decreased but that of feeding and pupal stages increased to sustain an overall high rate of generation survival. At the highest densities, survival in both stages declined and so, of course, did generation survival. Thus, in western spruce budworm, there was a compensatory relationship between these sequential survival rates over much of the range of outbreak densities, as was found in spruce budworm (Régnière and Nealis 2007), with the same overall result, relative stability in outbreak densities for several generations.

Dispersal of gravid moths bridges spatial variation in western spruce budworm densities via egg recruitment. We found a negative relationship between per-capita recruitment of eggs and the density of moths, as found by Campbell et al. (1983a), as well as by Greenbank (1963) for spruce budworm. Van Hezewijk et al. (2018) show trade-offs between size-related flight propensity and fecundity of individual western spruce budworm moths. At the population level, this should result in the greatest emigration of gravid moths at intermediate densities where moths are abundant and well-nourished. Consequently, a net exchange of moths between locations would be more difficult to detect during highly synchronized outbreaks when populations are at similar densities within a region (Régnière and Lysyk 1995), or where the number of locations sampled is few (Royama 1984). Recent evidence with more spatial elements and representing a greater range of the outbreak phase, including this study, show these exchanges are common and play an important role in the dynamics of outbreaks (Régnière et al. 2012, Régnière and Nealis 2019b).

Our primary study locations were early risers in the eventual, broader outbreak of the 2000s. Local outbreaks either resurged following initial collapse (Okanagan Valley) or remained at high population densities (Nicola Valley) for several years after generation survival began to decline, sustained by net immigration of gravid moths

from higher-density populations elsewhere. Once generation survival and mean moth density declined throughout the greater region, the influence of moth dispersal on recruitment waned and declining trends in generation survival dominated. Outbreaks collapsed over the entire region simultaneously and quickly. These direct measures of recruitment demonstrate that moth migration and consequent recruitment rates are density related and operate over long distances. It is now clear this process can amplify or dampen longer-term trends in generation survival with observable impacts on fluctuations in population densities.

CONCLUSIONS

This study enabled a comparative analysis of survival of related, conifer-feeding budworms during an outbreak. The analysis integrated time series of population change with independent models of processes considered important, and debatable, in budworm population dynamics. We conclude that a common sequence of trophic interactions, both bottom-up and top-down, drives characteristic outbreak patterns of budworms. Earlier hypotheses proposed that changes in the forest as a resource drive these fluctuations in population density (Morris 1963a, Ludwig et al. 1978). Our analysis reveals bottom-up mechanisms of change are important but more pervasive and their significant effects on survival occur earlier in the life cycle than previously thought. Variation in the emergent dynamics of these bottom-up ecological relationships is a function of spatial variation in forest characteristics coupled with a temporal change in the condition of those forests resulting from damage by the budworm itself. Temporal change in forest condition varies from immediate to long term but eventually reduces survival. Importantly, the rate of change in the relationship between survival of early-stage budworms and forest condition is related directly to host-specific vulnerabilities. The resulting density of feeding larvae determines, in turn, their susceptibility to other local processes, such as natural enemies, that ultimately determine generation survival.

The significance of differences in vulnerability among host trees allows generalization of a tri-trophic model to the dynamics of all conifer-

feeding budworms. It is a more robust thesis than simple predator-prey models (Royama et al. 2017) as it accommodates spatial and temporal variability in the resource mosaic without invalidating the complex role of natural enemies. As with changing rates of attack by natural enemies during the course of outbreaks, the effect of changing forest condition on survival is a function of budworm density, lagged in time, reinforcing the intrinsic ecological structure of oscillating populations (Royama 1992, Berryman 2002). Further, the sequence in which these specific density-related trophic interactions occur adds functional insight to Royama's (1992) notion of conditional equilibrium in which timing in the direction and rate of change in the population cycle are probabilistic on the status of other members of the food web. If a key element changes in the food web, a new, unique equilibrium could result. In Royama's view, however, the food web was restricted to the spruce budworm and its natural enemies. We see no theoretical inconsistency with including the resource as a food web element, conditioning the direction and amplitude of population fluctuations (Régnière and Lysyk 1995). Indeed, the inclusion of bottom-up processes reduces uncertainties impeding reconciliation of competing paradigms (Pureswaran et al. 2016).

This underscores the return of the host tree to the population ecology of conifer-feeding budworms and the motivation for the rich legacy of population studies: their spectacular outbreaks and disturbance to forests. The primary hosts of budworms appear equally susceptible to damaging infestations, but their vulnerability varies with true firs (*Abies*) more vulnerable than spruces (*Picea*), Douglas-fir (*Pseudotsuga*), and pines (*Pinus*). The greater vulnerability of true firs is obvious in forests on both sides of the continental divide. It is related to the greater palatability of old foliage on fir that extends the phenological window available to budworms compared with other host genera (Nealis 2019). Where forests are dominated by *Abies*, high tree mortality occurs in many stands (Morris 1963a, Maclean 1980), and local budworm populations collapse (Royama et al. 2017). The legacy of such a damaging outbreak will have a lasting, negative impact on recovery of budworm populations to the next outbreak (Berquet et al. 2021). By comparison, despite

the duration of the western spruce budworm outbreak investigated here, there was little tree mortality, a common pattern where Douglas-fir is the dominant forest component (Van Sickle 1987). This may be one of the reasons why western spruce budworm outbreaks have resurged several times since the 1970s in BC and remain a distinct possibility in the near future.

Finally, a comment on the effects of climate change. The recent outbreak of western spruce budworm examined here was the most extensive and persistent recorded in Western Canada, engulfing practically the entire range of the Interior Douglas-fir zone in BC (Maclauchlan et al. 2018). At the same time, areas of chronic historical outbreak are becoming less favorable as temperatures increase, while areas previously too cool become more susceptible to outbreaks (Régnière and Nealis 2019a). If these changes are the result of correlated trends in weather patterns directly affecting survival of budworms, population data presented here and associated modeling studies (Nealis and Régnière 2014, Régnière and Nealis 2019a), add insight to these complex phenomena. If changes in climate also stress trees and increase their nutritional quality for budworms throughout their range (White 2018), resulting disturbances could, or already have, become more frequent, extensive, and problematic.

The main insight for forest managers is that the geographic susceptibility to western spruce budworm is changing and more frequent outbreaks in northern and high-elevation forests with ample hosts may become the norm. The ecological processes determining population behavior examined here are not likely to change, but their interactions with changing climate and forest structure, whether caused by natural or anthropogenic changes, will continue to challenge and surprise resource managers for the foreseeable future.

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