

**LIFE HISTORY TRADE-OFFS IN HOST CHOICE FOR A SPECIALIST
FOLIVORE, SPRUCE BUDWORM (*CHORISTONEURA FUMIFERANA*)**

by

Lauren Stead

Bachelor of Science in Environment and Natural Resources, University of New
Brunswick

2019

A Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree of

Master of Science

in the Graduate Academic Unit of Biology

Supervisors: Stephen B. Heard, PhD, Biology
Robert Johns, PhD, Adjunct Professor, Biology

Examining Board: Cheryl Patten, PhD, Biology, Chair
Alexa Alexander, PhD, Biology
Kara Constanza, PhD, Forestry

This thesis is accepted by the Dean of Graduate Studies

THE UNIVERSITY OF NEW BRUNSWICK

August, 2019

© Lauren Stead, 2019

ABSTRACT

Spruce budworm, *Choristoneura fumiferana* Clem., is an important outbreaking pest in Atlantic Canada. It defoliates several coniferous tree species, including balsam fir, *Abies balsamea* (L.) Mill, and black spruce, *Picea mariana* (Mill.) Britton, Sterns & Poggenb.. Budworm is a flush feeder, meaning it feeds on the newest foliage as soon as the buds burst, and times its emergence from diapause accordingly. This emergence often lines up with that of balsam fir, but is asynchronous to its secondary host, black spruce, which bursts much later. This asynchrony with black spruce begs the question of why budworm would choose black spruce as a host if/when balsam fir is available. To better understand the consequences of host plant selection by budworm in the spring for feeding, as well as prior to overwintering, I completed field experiments to determine how host tree species influences the budworm performance during both the overwintering and feeding periods. I established weekly cohorts to put budworm on two host species, simulating a broad window of emergence from diapause, beginning a few weeks before expected budburst of balsam fir to a few weeks after budburst of black spruce. After pupation, I removed the budworm from branches they were on. I assessed bud stage of these host trees for each cohort and various performance measures of surviving budworm. Budworm on balsam fir had higher survival than those on black spruce. I also investigated budworm overwintering mortality on these same trees. In northern New Brunswick, I felled and collected various sections of the host trees including branches and trunks from the upper and middle crown in the spring prior to emergence from diapause. I collected emerging budworm from these tree sections and reared them so I could assess parasitism. Unless budworm emerge from diapause perfectly synchronous to balsam fir's budburst, black spruce is just as good of a

host for budworm to feed and overwinter on. Budworm overwintering on balsam fir had higher parasitism, likely due to its evolution with that host. There are ultimately trade-offs between overwintering mortality and having a superior quality food host. This study is the first to look at how these tri-trophic interactions may affect budworm host selection.

DEDICATION

I think it's only appropriate that I dedicate this thesis to the spruce budworm. I would not have gotten to where I am without you.

ACKNOWLEDGEMENTS

There are many people to whom I owe so much gratitude towards in helping me through this experience. Words cannot describe how thankful I am for them, but I will try my best.

First, I must thank my supervisors, Dr. Stephen Heard and Dr. Rob Johns. Your guidance, support and kind advice through my masters research made all of this possible. It was a privilege and honour for me to share your scientific knowledge. Your encouragement and jokes and sassiness made this all a little easier.

Thank you to my supervisory committee Les Cwynar and Michael Stastny for your advice throughout my thesis. And, also thanks to Les again for the boggle games.

Thank you to the nerds of the Heard variety: Jen Anderson, Rylee Isitt, Tony Einfeldt, Chandra Moffat, and Mischa Giasson for helping with field and lab work, for providing feedback on presentations and always being up for distractions and Grad House beverages.

Thank you, Joel Bates. for showing me how to be more organized when doing field work, for carrying my ladders for me, for almost getting hypothermia to get my field work completed, for literally having my back and smiling through it all.

Thank you, Katie Luiker, for all your help with my research and always being so positive even when it was cold and raining on us, and for showing me so many new podcasts.

Thank you to Fornebu Lumber Inc. for finding me a field site and cutting down my trees at lightening speed, especially to Emma Bell-Carruthers, Daniel Caissie, and Craig Jardine.

Thank you to Sara Edwards for helping me when I couldn't figure out my R code and explaining it to me so that I understood what was going on.

Thank you to everyone at the Canadian Forest Service- Atlantic Forestry Centre who helped me in the field and in the lab to get all my samples processed: Emily Owens, Benoit Morin, Keegan Moore, Clare Forbes, Holly Blaquiere, Sue He, Andrew Lewis, John McMullen, Josh Sandwith, Allyson Heustis, Katie Burgess, Megan Blanchard, Kendra Wagner, Sam Outhouse, Alex Mathisen, Katie Whittaker, Mariah Robichaud, Thomas Somers, Jordan Allen, Dibaba Ekangyela, Crystal Casey, Emily Papagiannis, Emma Bailey, Ifedayo Abel-Adegbit, Jessie Wilson, Madeline Honeyman, Michael Depow, Cameron Rugo and Neil Morash.

Thank you to my parents, Karen Stephen and Ian Stead, for being the so supportive and encouraging during this time. But that doesn't even begin to scratch the surface on how you guys have been so amazing.

Thank you, Mallory MacDonnell, for showing me how to do my own field work and for introducing me to the wonderful world of budworm and for supporting me in so many other ways.

Thank you to my roommates, Hilary Swan and Sara Taaffe, for so many things not limited to: lazy Sundays and family dinners, sharing your perspectives, putting up with me, destressing with me, learning to regurgitate a general summary of my research and just being two of the best people a girl could live with for 3 years.

I also owe a huge thanks to Stephanie Symons specifically for showing me short-cut keys on my keyboard, but so many other things as well. My coding in R would have been a lot more tedious without that knowledge.

Thank you to my siblings(-in-law) for listening and providing me with your sage advice, even though I'm convinced you still don't know what I've been doing for the past two years. And thank you to my nephews, Cooper, Henry, Theo, Charles, Malcolm and Gus for always being my comic relief.

TABLE OF CONTENTS

ABSTRACT	ii
DEDICATION	iv
ACKNOWLEDGEMENTS	v
TABLE OF CONTENTS	viii
LIST OF TABLES	ix
LIST OF FIGURES	x
CHAPTER 1-GENERAL INTRODUCTION	1
LITERATURE CITED	6
CHAPTER 2- LIFE HISTORY TRADE-OFFS IN HOST CHOICE FOR A SPECIALIST FOLIVORE, <i>CHORISTONEURA FUMIFERANA</i>	10
INTRODUCTION	10
METHODS	14
RESULTS	20
DISCUSSION	21
LITERATURE CITED	28
CHAPTER 3- GENERAL CONCLUSION	52
LITERATURE CITED	56
APPENDIX 1	58
APPENDIX 2	64

LIST OF TABLES

Table 1. Site Characteristics.....	40
Table 2. Total density of moths on individual trees from 2017 and 2018 overwintering distribution assessment (linear mixed effects model).....	41
Table 3. Overwintering survivorship and parasitism of balsam fir and black spruce from 2017 and 2018 (linear mixed effects model).	42
Table 4. Species breakdown of parasitism by the two most abundant parasitoids in 2017.....	43
Table 5. Spring survival and average female wing length from 2016 and 2017(linear mixed effects model).....	44
Table 6. Fitness per second-instar larva as the product of survivorship and per-survivor fecundity of all combinations of years from the overwintering distribution and spring emergence experiments.....	45

LIST OF FIGURES

Figure 1. Setup of second-instar larval emergence traps for spruce budworm.....	46
Figure 2. Total number of overwintering survivors combined with budworm larvae that died prior to emergence (extracted by a sodium hydroxide rinse) from the overwintering distribution assessment in a) 2017 and b) 2018.	47
Figure 3. Proportion of mortality (a) 2017 and c) 2018) and parasitism(b) 2017 and d) 2018) between balsam fir (○) and black spruce (●) and in different parts of the tree crown.....	48
Figure 4. Proportion of parasitism on the two hosts, and canopy positions by specialist parasitism in 2017.....	49
Figure 5. Proportion of survivorship (a) 2016 and c) 2017) and female moth wing length (b) 2016 and d) 2017) for budworm between balsam fir (○) and black spruce (●). Arrows indicate budburst for the corresponding species.....	50
Figure 6. Fitness estimate from the 2017 early and late spring emergence experiment and 2017 overwintering mortality experiment. Arrows indicate budburst for the corresponding species.	51

CHAPTER 1-GENERAL INTRODUCTION

LAUREN STEAD

Department of Biology, University of New Brunswick, PO Box 4400, Fredericton, New Brunswick, E3B 5A3

Natural selection shapes life history strategies over time to better suit an organism to its environment. For an organism to optimize its ability to survive to reproductive age, find a mate, and produce offspring, it must respond to factors such as abiotic conditions, food availability and pressure from natural enemies. Foraging strategies may also change as a result of ecological trade-offs between these factors and some animals may risk reduced performance with respect to one factor if it confers higher overall performance associated with all other factors. For example, baboons (*Papio cynocephalus ursinus*) will avoid food-rich habitat if the risk of exposure to leopards is high, and instead feed in low-risk relatively food-poor habitat (Cowlshaw, 1997). Juvenile coho salmon (*Oncorhynchus kisutch*) are less likely to travel long distances to obtain prey after they have encountered a potential predator, compared with those that have never had such an encounter (Dill & Fraser, 1984). Elucidating and quantifying these trade-offs may help resolve many puzzling foraging decisions underlying the ecology of even well-studied species.

I examined foraging decisions and performance trade-offs for the spruce budworm, *Choristoneura fumiferana* Clem. (hereafter budworm). Budworm is an outbreak defoliator of the boreal and mixed temperate forests, feeding primarily on balsam fir (*Abies balsamea* (L.) Mill) and white spruce (*Picea glauca* (Moench) Voss) (Boulanger & Arseneault,

2004). While budworm larvae tend to prefer feeding on balsam fir and white spruce they are also known to feed on red spruce red spruce (*Picea rubens* Sarg.) and black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.). In late July and early August, budworm moths lay eggs which hatch within 8 to 12 days. Budworm larvae disperse on the branch and spin a hibernacula where they overwinter as a second instar (L2) (Royama, 1984). In the spring, the L2 emerge and begin feeding on the new growth and moult until the sixth instar. By mid-July, budworm will begin to pupate and emerge as moths by late July and early August. The moths are active for up to two weeks to mate and lay eggs (Morris, 1963).

The literature has primarily focused either on overwintering survival in laboratory experiments (Han & Bauce, 1995, 1998) or on the feeding period (Fuentealba et al., 2017; Lawrence et al., 1997), and has not assessed these two life stages as a whole. Combining these two life stages provides a more complete understanding of budworm life history and the trade-offs that may be occurring. I ran two experiments to assess performance on two hosts (balsam fir and black spruce) across the life cycle of budworm. In one experiment, I examined the phenological window of spring-time emergence from diapause and how different hosts and timing of budburst influence the survival of budworm. In the other experiment, I looked at where budworm are choosing to spin their hibernacula and overwinter, and the associated costs of those decisions. I combined the results of these two experiments to create an estimate on overall budworm fitness on both hosts.

Lawrence et al. (1997) showed that budworm performance on white spruce was highly related to budburst of their host, with performance being highest one week prior to burst. Mattson et al. (1983) reported that larvae feeding on balsam fir tend to have higher

survival and larger adult body size, compared with those feeding on black spruce. This emergence from diapause and synchrony to budburst is likely due to the decline in foliage quality that occurs shortly after budburst (Feeny, 1970). Asynchrony of emergence and budburst may lead budworm to mine one to two-year-old foliage, until the buds flush, as L2 are unable to enter enclosed buds (Desbiens, 2006). If budworm feed on the old foliage for too long, they risk reduced survival and growth (Blais, 1952; Mattson et al., 1983). It is important for budworm to emerge in synchrony with the budburst of their hosts. Black spruce undergo budburst 10-14 days later than balsam fir and white spruce (Blais, 1957; Chrosciewicz, 1986). Consequently, budworm typically align their emergence one week prior to budburst of white spruce or balsam fir (Blais, 1957; Volney & Cerezke, 1992), resulting in a substantially longer period between when larvae become active and budburst occurs on black spruce. For this reason, black spruce is generally considered an inferior host for budworm to feed on.

Little is known about the link between overwintering distribution of budworm as L2 and associated survival, especially in terms of how it might vary within and among potential host trees. Eveleigh & Johns (2014) reported that during most developmental stages, budworm tend to occur at higher densities in the upper compared to the lower crown; however, L2 tend to occur at higher densities in lower crown levels. This distribution may in part reflect dispersal of the neonate (newly hatched) larvae, as they attempt to find overwintering sites on the branches and bark of the lower crown (Miller & Kettela, 1972; Eveleigh & Johns, 2014). In a close relative, the western spruce budworm (*Choristoneura occidentalis* Freeman), the L2 will travel from the branch tips towards the trunk in an effort to find adequate shelter for overwintering on Douglas fir (*Pseudotsuga*

menziesii (Mirb.)). Such dispersal is potentially dangerous and increases chances of mortality, such as exposure to natural enemies. However, the potentially superior shelter provided may outweigh risks (Nealis & Régnière, 2016).

In my thesis, I carried out surveys and bioassays to determine the overwintering distribution during the L2 stage and survival of subsequent feeding instars. I hypothesized that those that overwinter closer to the bole may have greater chance of survival throughout the winter than those that are on the branch tips because of increased shelter (i.e. denser foliage in which to hide). For comparison, the western spruce budworm has higher survival in sites where the temperature is lower (Nealis & Régnière, 2016). For this particular species, survival was significantly higher on the bole than the branches, and at higher than at lower elevations (Nealis & Régnière, 2016). Seeking these more suitable overwintering sites protects budworm from abiotic extremes and may improve their resilience to stresses they might experience while in their hibernacula. This might increase their survival potential over diverse spatial and temporal scales (Nealis & Régnière, 2016). The risks of travelling closer to the bole are offset by the reward of finding suitable overwintering sites (Nealis & Régnière, 2016).

Top-down influences associated with parasitoids may influence overwintering distribution and survival. Budworm has two primary parasitoids that attack the neonate larvae, or larvae that have just spun their hibernacula: *Apanteles fumiferanae* Vier and *Glypta fumiferanae* (Vier). These parasitoids overwinter in the budworm host and emerge in later instars (fourth-sixth), with *Apanteles* emerging slightly earlier than *Glypta* (Lewis, 1960). Parasitism by *Apanteles* is greater in the upper crown, but no significant variance has been observed in crown level of other parasitoids of budworm (Eveleigh & Johns,

2014). It is speculated that this upper crown bias may be due to relatively higher budworm densities in the upper crown, as well as fewer spots for the larvae to conceal themselves, such as in crevices and lichens. Although there are many other parasitoids of budworm, including *Tranosema rostale* (Brischke), which has been observed in lower endemic populations (Seehausen et al., 2016), *Apanteles* and *Glypta* were the two most common found in the present study.

In addition to examining the overwintering distribution of budworm, I also sought to understand whether trade-offs occur in host choice in these two life stages. For this aspect of my thesis, I tested two hypotheses: (1) budworm favour feeding on balsam fir and thus more budworm will overwinter there as L2 and (2) budworm performance (wing length, a proxy for fecundity) will change when newly emerged larvae are challenged with foliage at different stages of bud development. I predict that these challenges will be more onerous on black spruce than balsam fir, because of the delayed budburst in black spruce.

Author Contributions:

The original experimental design for chapter 2 was conceived by Stephen Heard and Rob Johns. I was responsible for organizing fieldwork, field setup, insect collection, analysis of the data, and writing of the manuscripts.

LITERATURE CITED

- Blais, J. R. (1952). The relationship of the spruce budworm (*Choristoneura fumiferana*, Clem.) to the flowering condition of balsam fir (*Abies balsamea* (L.) Mill.). Canadian Journal of Zoology, 30 (1), 1–29. <https://doi.org/10.1139/z52-001>
- Blais, J. R. (1957). Some relationships of the spruce budworm, *Choristoneura fumiferanae* (Clem.) to black spruce, *Picea mariana* (Moench) Voss. The Forestry Chronicle, 33, 364–372. <https://doi.org/10.5558/tfc33364-4>
- Boulanger, Y., & Arseneault, D. (2004). Spruce budworm outbreaks in eastern Quebec over the last 450 years. Canadian Journal of Forest Research, 34(5), 1035–1043. <https://doi.org/10.1139/x03-269>
- Chrosciewicz, Z. (1986). Foliar moisture content variations in four coniferous tree species of central Alberta. Canadian Journal of Forest Research, 16(1), 157–162. <https://doi.org/10.1139/x86-029>
- Cowlishaw, G. (1997). Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. Animal Behaviour, 53(4), 667–686. <https://doi.org/10.1006/ANBE.1996.0298>
- Desbiens, M (2006) Relation phénologique entre le débourrement des bourgeons chez le sapin baumier et l'émergence des larves de deuxième stade de la tordeuse des bourgeons de l'épinette, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). MSc thesis, Department of Forestry, Université Laval, Quebec, Canada

- Dill, L. M., & Fraser, A. H. G. (1984). Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). *Behavioral Ecology and Sociobiology*, 16(1), 65–71. <https://doi.org/10.1007/BF00293105>
- Eveleigh, E. S., & Johns, R. C. (2014). Intratree variation in the seasonal distribution and mortality of spruce budworm (Lepidoptera: Tortricidae) from the peak to collapse of an outbreak. *Annals of the Entomological Society of America*, 107(2), 435–444. <https://doi.org/10.1603/AN13136>
- Feeny, P. (1970). Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology*, 51(4), 565–581. <https://doi.org/10.2307/193403>
- Fuentealba, A., Pureswaran, D. S., Bauce, É., & Despland, E. (2017). How does synchrony with host plant affect the performance of an outbreaking insect defoliator? *Oecologia*, 184(4), 847–857. <https://doi.org/10.1007/s00442-017-3914-4>
- Han, E.-N., & Bauce, É. (1995). Glycerol synthesis by diapausing larvae in response to the timing of low temperature exposure, and implications for overwintering survival of the spruce budworm, *Choristoneura fumiferana*. *Journal of Insect Physiology*, 41(11), 981–985. [https://doi.org/10.1016/0022-1910\(95\)00049-Z](https://doi.org/10.1016/0022-1910(95)00049-Z)
- Han, E.-N., & Bauce, É. (1998). Timing of diapause initiation, metabolic changes and overwintering survival of the spruce budworm, *Choristoneura fumiferana*. *Ecological Entomology*, 23(2), 160–167. <https://doi.org/10.1046/j.1365-2311.1998.00111.x>

- Lawrence, R. K., Mattson, W. J., & Haack, R. A. (1997). White spruce and the spruce Budworm: defining the phenological window of susceptibility. *The Canadian Entomologist*, 129(2), 291–318. <https://doi.org/10.4039/Ent129291-2>
- Lewis, F. B. (1960). Factors affecting assessment of parasitization by *Apanteles fumiferanae* Vier. and *Glypta fumiferanae* (Vier.) on Spruce Budworm Larvae. *The Canadian Entomologist*, 92(12), 881-891. <https://doi.org/10.4039/Ent92881-12>
- Mattson, W. J.. 1983. Spruce budworm (*Choristoneura fumiferana*) performance in relation to foliar chemistry of its host plants. In: Talerico, Robert L.; Montgomery, Michael, tech. coords. Proceedings, forest defoliator--host interactions: A comparison between gypsy moth and spruce budworms; 1983 April 5-7; New Haven, CT. Gen. Tech. Rep. NE-85. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station: 55-65.
- Miller, C. A., & Kettela, E. G. (1972). An additional note on sampling overwintering spruce budworm larvae. Fredericton, NB. Information Report M-X-34. 13 p.
- Morris, R. F. (1963). The dynamics of epidemic spruce budworm populations. *Entomological Society of Canada*, 95, 1-12. <https://doi.org/10.4039/entm9531fv>
- Nealis, V. G., & Régnière, J. (2016). Why western spruce budworms travel so far for the winter. *Ecological Entomology*, 41(5), 633–641. <https://doi.org/10.1111/een.12336>

- Royama, T. (1984). Population dynamics of the spruce budworm *Choristoneura fumiferana*. *Ecological Society of America*, 54(4), 429–462.
<https://doi.org/10.2307/1942595>
- Seehausen, M. L., Labrecque, M., Martel, V., Régnière, J., Mansour, A., & Smith, S. M. (2016). Reproductive biology and behavior of *Tranosema rostrale* (Hymenoptera: Ichneumonidae), a parasitoid of low-density spruce budworm (Lepidoptera: Tortricidae) Populations. *Journal of Insect Behavior*, 29(5), 500–514.
<https://doi.org/10.1007/s10905-016-9576-y>
- Volney, W. J. A., & Cerezke, H. F. (1992). The phenology of white spruce and the spruce budworm in northern Alberta. *Canadian Journal of Forest Research*, 22(2), 198-205. <https://doi.org/10.1139/x92-026>

CHAPTER 2- LIFE HISTORY TRADE-OFFS IN HOST CHOICE FOR A SPECIALIST FOLIVORE, *CHORISTONEURA FUMIFERANA*

LAUREN STEAD¹, STEPHEN B. HEARD¹, AND ROBERT C. JOHNS²

¹Department of Biology, University of New Brunswick, PO Box 4400, Fredericton, New Brunswick, E3B 5A3

²Natural Resources Canada, Canadian Forest Service, Atlantic Forestry Centre, Fredericton, New Brunswick, E3B 5P7

INTRODUCTION

Animals across a range of taxa are under heavy selective pressure to make foraging decisions that enhance their performance, or that of their progeny (Donelan & Trussell, 2015). Numerous studies on insects whose young are constrained to feed at the site selected by the mother (e.g., gallers, miners, and borers) indicate strong selection for mothers to select plant modules that confer relatively high fitness to progeny (Price et al., 1987; Craig et al., 1989). For example, female gall-making insects tend to select hosts or plant modules that will provide their offspring with adequate food resources and protection from natural enemies (Craig et al., 1989). Some shoot-borers select more robust terminal shoots as they tend to be more favorable for larval development under high infestations (Sower & Mitchell, 1987). In other insect guilds where progeny are free-feeding, mothers may face similarly strong selective pressure to make adaptive oviposition decisions for their progeny (Kessler & Baldwin, 2002). However, larvae may also experience pressure to later shift where they feed as a means of compensating for sub-optimal decisions by the mother (Mayhew, 2001), phenological changes in host plant quality (Feeny, 1970), changing larval

nutritional needs during development (Hochuli, 2001), or potential risks of exposure to natural enemies (Rabb & Bradley, 1968; Donelan & Trussell, 2015).

While many studies have focused on foraging decisions made by individual life stages, comparatively few span foraging decisions made across multiple life stages. The few studies that have done so suggest that the collective foraging decisions of both mothers and progeny may be essential in some species for maintaining high performance. In forest ecosystems, relatively few studies have examined the cumulative impacts of host selection across multiple life stages, although several recent examples have studied foraging within individual host trees. For example, *Pikonema alaskensis* (Roh.) mothers lay eggs in the base of buds in lower crown branches, which provides neonate larvae access to nutritious newly burst shoots (Katovich et al., 1995). However, as larvae develop they shift to larger, more nutritious shoots in the upper crown and at branch tips, which collectively leads to higher overall survival, especially among females (Johns et al., 2009; Johns et al., 2010). Similarly, adults of *Zeiraphera canadensis* Mut. & Free. lay their eggs in the remnants of current year bud scales of white spruce for access to the foliage as soon as it bursts. Acropetal (outward towards the shoots) dispersal in later instars leads to higher survival, larger growth and faster developmental rate (Carroll & Quiring, 1994).

In this study, I examined the foraging preferences and associated performance of the eastern spruce budworm (*Choristoneura fumiferana* Clem.) (hereafter budworm) throughout its larval development on two of its potential host trees. Budworm is the foremost outbreaking defoliator of spruce (*Picea* spp.) and balsam fir (*Abies balsamea* (L.) Mill) in the boreal and mixed temperate forests of North America (Boulanger & Arseneault, 2004). Several studies have shown that budworm has higher survival and larger

body size when feeding on balsam fir or white spruce compared to black spruce (Mattson et al., 1983). Recent studies suggest that at least some of the differences in host nutritional quality are associated with phenology. Budworm is a spring-feeding insect and feeds on newly burst foliage, although larvae will backfeed on older foliage when new foliage is unavailable (Trier & Mattson, 1997; Régnière & Nealis, 2007). The timing of budworm larval emergence in spring is closely synchronized with budburst, especially that of balsam fir and white spruce, which occur at roughly the same time. Black spruce, however, bursts nearly 10 days later and thus larvae overwintering on that host may be forced to spend an extended time either starving or mining mature needles, with associated costs to growth and survival (Blais, 1957). As such, one might expect heavy selective pressure for mothers to lay eggs on balsam fir or white spruce and to generally avoid black spruce. However, black spruce is a common host even when balsam fir is available, and this leaves open questions around whether there are advantages to oviposition on black spruce (Blais, 1957; Hennigar et al., 2008).

Most studies on budworm dynamics have tended to focus on feeding larvae, largely ignoring what happens during their overwintering stage. Two main life stages during which budworm makes foraging decisions influence its distribution among host trees. First, in mid July after emerging from the pupae, female moths mate and select a host upon which to lay their eggs. Eggs are often laid in clusters on the foliage (Morris, 1963). Weeks later, when the eggs hatch, the first-instar larvae have a second opportunity to redistribute both within and among crowns (Johns & Eveleigh, 2012). Since the larvae do not feed in this life stage, diet quality is not an immediate concern. However, these host trees may still vary in terms of the availability of suitable microhabitats for overwintering or areas that

are protected from parasitoid attack. Larvae may “balloon” (dispersing via wind on a silken thread) to neighbouring trees or nearby stands. This is risky and undirected, but may be necessary if the mother chose an unsuitable host or if competition is high (Morris, 1963; Johns & Eveleigh, 2013). The primary parasitoids during this period are *Apanteles fumiferanae* Vier. and *Glypta fumiferanae* (Vier.) (Royama, 1984). In diapause and until even after they spin a hibernaculum, the L2 may be attacked by parasitoids which are active from the time of moth flight to when hibernacula have been spun, although they most often attack the neonate larvae shortly after egg eclosion (Lewis, 1960). When L2 emerge and search for feeding sites in the spring, the quality of their host is important as they seek the newly burst high quality foliage. Budworm may balloon in this life stage as well in search for higher quality food, however, walking around is more common (Johns & Eveleigh, 2013). Although several studies have examined how foliage nutritional quality varies between different potential hosts for budworm (Mattson et al., 1983), much less work has examined potential differences in natural enemy impacts; yet, natural enemies are one of the main drivers behind outbreak cycles (Royama, 1984; Régnière & Nealis, 2007). I focused on parasitism during the overwintering stages and host quality during the spring, from the time that the eggs hatch to the time that they emerge in the spring to feed.

Here, I discuss a series of field studies carried out to better understand the consequences of host plant selection by budworm prior to overwintering, as well as in the spring for feeding. I carried out experiments to determine how host tree species influences the performance of budworm during the overwintering period through larval feeding in the subsequent year. I hypothesized that budworm prefer feeding on balsam fir and therefore mothers will select it as the host for egg lay (using L2 distribution as a proxy). I asked

whether the feeding advantage on balsam fir versus black spruce is balanced by other factors, such as mortality from higher parasitoid attack. For spring feeding, I hypothesized that budworm will differ in performance when newly emerged larval cohorts are challenged with foliage at different stages of bud development and that these challenges will be more obvious on black spruce than balsam fir, because of the delayed budburst in black spruce. I predicted that budworm will have higher survival on balsam fir during this feeding period, but that there may be other survival advantages to overwintering on black spruce that offset cost incurred during the subsequent feeding period.

METHODS

Study Species

In late July to early August, budworm moths emerge from their pupae and live for up to two weeks, during which they mate and lay eggs (Morris, 1963). After egg hatch, larvae moult, disperse on the branch or balloon to neighbouring trees, and then spin a hibernaculum in which to overwinter as second-instar larvae (L2). Budworm do not feed from when they hatch in the summer until the following spring; therefore, they must rely solely on the resources they acquire from the egg (Miller, 1958; Royama, 1984; Nealis & Régnière, 2016). In the spring, L2 emerge and begin feeding on the new foliage and moult until they are sixth-instar larvae. By mid-July, budworm begin to pupate and generally remain in that phase for approximately 10 days before emerging as a moth (Morris, 1963).

Overwintering distribution and mortality

To determine how host tree species influences budworm density and performance during the overwintering period (i.e. pre-feeding), I conducted field surveys in two

different locations in 2017 and 2018. Because budworm may overwinter on different parts of the tree crown, I also stratified collections between different crown levels and within the crown levels (i.e. trunk and branches), going beyond standard survey protocol used in budworm monitoring (REF). Sites for surveys were selected along the leading edge of an ongoing budworm outbreak, where previous defoliation was limited and population densities were low to moderate compared with the peak densities commonly observed during outbreaks (Table 1). Stands were composed of an even mix of balsam fir and black spruce, *Picea mariana* (Mill.) Britton, Sterns & Poggenb., that were 25-30 years in age and 15-25 m in height.

To ensure collected budworm were overwintering on the host we retrieved them from, we needed to obtain our samples prior to L2 emergence. Budworm require a minimum threshold of degree-day accumulation to emerge from their hibernacula so I used degree-day accumulations to determine when to collect branches to anticipate natural timing of emergence (Baskerville & Emin, 1969). In Charlo, New Brunswick where my sites were located, the budworm require 37 degree days above 6°C (Baskerville & Emin, 1969; Volney & Cerezke, 1992). I obtained the daily minimum and maximum temperatures beginning on March 1 for sites 1 and 2 as no degree days had accumulated before that date (Environment Canada Historical Weather Data, 2018). Using the degree day model, I was able to calculate when budworm L2 would be emerging on the selected site in the spring, April 23, 2017 and May 3, 2018.

One week prior to the model's predicted L2 emergence, I randomly selected and felled 10 healthy balsam fir and black spruce (Table 1). I divided each tree into thirds based on the length of the vegetative crown and sampled branches and bole sections from the

upper and middle sections. In total, I collected four different sections of tree: upper-crown branch, middle-crown branch, upper-crown bole, and middle-crown bole. The upper and middle branches were further divided into the base and tip of the branch, with each section measuring 45 cm in length. I separated tree sections in individual paper bags and brought them back to the Atlantic Forestry Centre (Canadian Forest Service, Fredericton, NB) rearing facilities for the larvae to emerge. Sections were held in a cold room at 4°C for under a week until they could be set up for lab rearing.

In the lab, I wrapped each individual tree section in paper towel, with an opening at the top, thickest end. I hung the wrapped sections 12" apart to prevent larvae from ballooning among samples and set a light on a 12-hour timer to simulate day-night cycles. Room temperature was kept at 22°C. On the string that the tree section was suspended from, I attached a small plastic cup to trap the larvae as they moved towards the light (Fig. 1). To prevent the samples from drying out, I soaked the wrapped tree sections in water, twice daily, until the paper towel was dripping. I then checked the cups, string and outside of the paper towel for emerged larvae twice daily until larvae were no longer emerging. All emerging larvae were placed into individual cups with ¾ oz McMorran diet (McMorran, 1965). I changed the diet as needed (e.g. if the diet turned brown or was mostly consumed) until pupation. Pupae were placed in empty cups until moth emergence. I measured the wings, sexed all adults and recorded mortality of all other life stages. A larva on a branch could have one of four fates: emergence as an adult, mortality due to parasitoid attack, mortality during overwintering in the hibernaculum, or mortality while feeding on diet (i.e. source of mortality unknown). Because larvae were only exposed to the natural environment during their overwintering phase, only two parasitoids were expected to be

observed (i.e., *Apanteles fumiferanae* and *Glypta fumiferanae*).

After three days without larval emergence, I removed the branches and boles from the paper towel and soaked the boles and branches in 1% sodium hydroxide for two hours to dissolve the hibernacula and release any overwintering second instar budworm remaining on each tree section. That was followed by a hexane rinse to separate the larvae from other organic material. I poured the effluent onto filter paper, so that the extracted larvae could be counted underneath a microscope (Harvey, 1957). This method allowed us to determine the number of larvae that did not emerge from hibernation to measure overwintering mortality.

I analyzed whether adult parasitism, overwintering mortality and density varied between balsam fir and black spruce, as well as by the location within the canopy, using a linear mixed effects model (R package: nlme). I dropped any interactions between species and set-up date that were not significant ($p > 0.05$). Species and location were treated as fixed effects and replicate tree was a random effect. All analyses were run in R version 3.3.3 (R Core Team, 2017).

Larval feeding performance

To determine how host species influences feeding larvae performance (i.e. spring survival), I conducted field bioassays in the spring of 2016 and 2017, across an extended phenological window to assess the complete budworm emergence period and how performance changes across different emergence times. Sites were in Noonan, New Brunswick at two different locations within the Canadian Forest Service's Acadia Research Forest (Table 1). I selected stands that were 25-30 years old with a mix of balsam fir and black spruce. I obtained wild L2 budworm contained in gauze sheets from Entomological

Research Services Incorporated (Fredericton, NB). At the study site, I selected 15 trees each of balsam fir and black spruce (Table 1). Starting April 28 in 2016 and May 4 in 2017, I pinned a section of the gauze sheets containing five larvae onto the branch tip of each tree in the mid-crown. I measured the branch to 50 cm and enclosed it in a fine-mesh cloth sleeve bag, which contained the budworm but excluded natural enemies. Cohort setups occurred weekly from late April to early June, simulating matches and mismatches in timing between emergence and budburst.

I pruned the branches in order of the weekly setup date (cohort) when most larvae had pupated (July 15-28), and brought them back to a laboratory for processing. After each sleeve cage was removed I collected all budworm stages. I stored pupae in sealed individual containers until moth emergence. I placed the remaining larvae onto foliage collected from their natal field site, replacing the foliage as needed until the larvae pupated, then transferred the pupae into individual containers. I set the containers of pupae and larvae underneath a light set on a 10-hour timer in a 22°C room. I counted, sexed and measured the wing lengths of all adults at collection (a proxy for potential fecundity), or once they emerged from their pupae. I used Auger's scheme for determining budburst development: "Stage 1, no apparent bud development (bud in winter condition); Stage 2, buds swelling and 10–35% of the needles visible; Stage 3, budburst, all needles visible but not flaring; Stage 4, needles flushing and flaring and shoot elongation initiated; Stage 5, shoots are supple and undergoing elongation" (Dorais and Kettela, 1982). I calculated budburst when 50% of buds were categorized as stage 4 (Fuentelba et al., 2017).

For each year, I analyzed whether survivorship and an estimate of expected fitness (see below) depended on tree species, cohort, and their interaction, using a linear

mixed effects model (R package: nlme). Species and cohort were treated as fixed effects and replicate tree as a random effect. In both years, survival data were zero-inflated so I broke the survivorship analysis into two stages. First, I used a linear mixed effects model to ask whether species and cohort could explain pattern in the loss of whole clutches (i.e., survivorship zero vs. non-zero). Second, I used a second linear mixed effects model to compare, across treatments, survivorship rates among replicates with non-zero survivorship. Because the two analyses led to identical interpretations, I chose to run a single analysis of the pooled survival data. I used a linear mixed effects model (R package : nlme) to determine the effect of species and simulated emergence date (cohort) on adult budworm performance (wing length). For the 2017 data, I pooled the sites after conducting an ANOVA that suggested that there was no significant site effect.

Host suitability: integrating budworm survival and performance measures

To determine how host species influences the life history of budworm performance, I integrated results from our overwintering survival and larval feeding assessments to estimate potential fitness for female larvae. Additionally, I assessed the potential fitness across the complete budworm emergence period and how that might change for budworm emerging at different times around the budburst of both hosts. I combined results from overwintering survival and larval feeding and estimated fitness for female larvae placed on foliage on a particular date and on either of the two hosts. I estimated fitness per L2 as the product of the overwintering survivorship, the cohort-specific spring survivorship and the cohort-specific average adult female wing length (Thomas et al., 1980). The result is a fitness estimate for moths for each spring emergence

cohort on each of the two tree host species. Because I ran two experiments, in two different years, I ran an analysis on combinations of all years from both experiments. I used the calculation to determine if fitness is dependent on tree species and cohort (simulated emergence time) using a linear mixed effects model, with branch as the replicate. I treated species and cohort as fixed effects and replicate tree as a random effect.

RESULTS

Overwintering distribution and mortality

In both years, budworm densities were significantly higher in the upper crown than the lower crown, however there was no effect of tree species (linear mixed-effects model; Fig. 2; Table 2). There was no significant effect of tree species or crown level on overwintering mortality in either year (Table 3, Fig. 3 a, c). Non-parasitoid mortality masks the fact that total mortality was higher as a result of parasitism, just not significantly. In 2017, parasitism was significantly higher on balsam fir compared to black spruce. Parasitism was higher in the upper crown in both tree species (Table 3; Fig. 3b). Trends were similar in 2018 (Fig. 3d). The two main parasitoid species of budworm that I collected, *Apanteles* and *Glypta*, together were significantly more abundant in the upper crown (Table 4; Fig. 4). *Apanteles* trended towards being found more on larvae from balsam fir, although the effect was marginal and statistically non-significant (Fig. 4).

Larval feeding performance

There was no interaction between tree species and timing of feeding initiation (cohort), so I dropped the interaction for both survival and average number of eggs laid. Survival was higher on black spruce for only one cohort (the final one of 2017; Fig. 5c).

Ignoring cohort, spring survival was significantly higher in balsam fir in both years (Table 5; Fig. 5 a, c for 2016 and 2017). Cohort had a significant effect on budworm survival (Table 5). Larval survival peaked for balsam fir in the middle cohort, which coincides with the timing of budburst (Fig. 5). The peak of survival was later in black spruce, compared to balsam fir, by one week in 2016 and two weeks in 2017. Female budworm developing on black spruce and fir had significantly longer wings in the earliest cohort than the last, by 13% and 11% respectively (2017 only). There was no effect of cohort on female moth wing length (potential fecundity) in 2016 (linear mixed-effects model; Fig. 5; Table 5).

Effects of host tree on overall fitness

When taking both overwintering survival and spring feeding into account but integrating across all cohorts, budworm did slightly better on balsam fir (Fig. 6). Averaging across all cohorts, budworm on fir had 10% higher fitness than their black spruce counterparts. However, considering cohort-specific fitness provides a more complicated picture, matching budburst to either species makes a major difference. In 2017, the week after balsam fir budburst, budworm on that host had 44% greater fitness than those feeding on black spruce (cohort 4). However, the week after black spruce budburst, budworm on spruce had 33% greater fitness (cohort 7). Relative to balsam fir, grouping cohorts in pre-budburst, budburst and post-budburst categories, trends showed a 3% increase, 24% decrease, and 6% increase from balsam fir to black spruce, respectively. These results were consistent across both years. The 2017 spring emergence survivorship showed a marginal effect of cohort on budworm fitness (Table 7).

DISCUSSION

My study suggests that overwintering on balsam fir puts budworm larvae at greater risk of parasitism associated with its two main specialist parasitoids, *Apanteles fumiferanae* and *Glypta fumiferanae*, that attack the overwintering stage. Natural enemies are important for understanding the role multi-trophic interactions play in budworm dynamics. Similar to our study, previous studies have also indicated that both *Apanteles* and *Glypta* have a bias budworm found in the upper crown of balsam fir (Miller, 1959, 1960; Dodge, 1961). A 1975 study (Simmons et al.) found that both *Apanteles* and *Glypta* are unable to detect tree species influence, however, it is still unknown if the parasitoids can detect semiochemicals of their hosts or volatiles of their hosts' hosts, as has been observed in other parasitoids (Vinson, 1976). Most studies examining these hymenopteran parasitoids have found more *Apanteles* in northeast North America whereas western studies find more abundant populations of *Glypta* (Dodge, 1961). I obtained similar densities of both species. It is possible that this reflects the trends seen in rising populations of budworm. This could partly be because budworm has evolved mainly with balsam fir and white spruce; as such, the parasitoids may be more quick to cue on budworm while feeding on those species in comparison to black spruce.

Budworm feeding on balsam fir had higher larval survival than those on black spruce (ignoring the within-season variation). Similarly, Fuentealba et al. (2017) showed that budworm on balsam fir trended towards higher survival than those on black spruce. After budburst in black spruce, budworm had higher survival on black spruce than fir, indicating that optimal timing relative to budburst is critical for budworm survival. On white spruce, budworm emerging 1-3 weeks prior to budburst had the highest survival, which may be consistent with balsam fir as budburst has similar timing (Chrosciewicz,

1986; Lawrence et al., 1997). They may have to mine less nutritious one-year-old foliage briefly, but it may be adequate to sustain them until new foliage becomes available. Lower survival of the earliest cohorts may be a result of extended feeding on old foliage. Although our L2 spring feeding study allowed larvae to feed immediately upon emergence, factors in nature can result in significant asynchrony between budburst of their host and L2 emergence. My experiment used controlled emergence dates to avoid confounding emergence with other factors. Among surviving budworm, later emerging females had shorter wing lengths (in 2017 only; Table 2; Fig. 2). Smaller wings tend to correlate to smaller female size, which in turn are likely to have lower fecundity (Calvo & Molina, 2005). Those budworm that are present may have the first access to resources available and may deplete them for those that emerge later. Reduced performance of late-emergers may impact the chances of overwintering survival for their offspring.

Optimal budworm emergence time on each host species for feeding occurred one week before budburst, which is consistent with past studies (Blais, 1952; Lawrence et al., 1997). This relationship corresponds with other literature looking at the phenological window of budworm emergence and its flush-feeding behavior (Lawrence et al., 1997; Trier & Mattson, 1997; Volney & Cerezke, 1992). Like budworm, the spring-feeding geometrid moth, *Epirrita autumnata*, is an outbreaking folivore. High population densities result in severe defoliation of mountain birch (*Betula pubescens* ssp. *tortuosa*), which then causes the birch to delay its budburst phenology in the spring (Haukioja et al., 1988; Tuomi et al., 1989). When hosts are defoliated, and thus larval competition is enhanced, adults may oviposit their eggs later in the fall, thereby delaying egg hatch in the spring. This delayed egg hatch confers larger pupae of *E. autumnata*, as it aligns the synchrony of its

spring emergence and host's budburst, providing the larvae with the freshest foliage (Kaitaniemi et al., 1997). For an insect, matching the phenology of its host is important for the entire life cycle.

Our study shows a more complicated dynamic than has been described previously in past studies focused on bottom up effects of balsam fir versus black spruce (Fuentelba et al., 2017). Budworm may face opposing selective pressures from bottom-up and top-down factors when selecting a host tree. Budworm risk exposing their eggs to higher parasitism if they choose to lay on balsam fir, but if those eggs survive, they find themselves in spring on a host that is superior for feeding. The opposite is true for females that choose to lay their eggs on black spruce. Our cohort-average fitness estimates suggest that there is no real difference in host selection for the female moths to lay their eggs. The optimal conditions, in light of a trade-off, are likely dependent on the timing of emergence in the spring. Given the average fitness difference between overall performance on black spruce and fir, female behaviour may favour one host over the other as an oviposition substrate – even given the superiority of fir for feeding. However, it is also important to note that in the relatively short life history of budworm and fast mating soon after emergence could mean that eggs end up more often on or near the female pupation host. Of course, a female could achieve higher fitness if she could select both a host (fir) and an emergence window for her offspring (one week before budburst) (Lawrence et al., 1997); but little is known about genetic control over emergence timing. The best-case scenario may be for a female to lay her eggs on both balsam fir and black spruce. However, L2 do have some options to disperse within and between hosts via ballooning, albeit at significant risk. Budworm larvae will balloon more when on poor host trees (i.e. those degraded by

previous defoliation) (Nealis & Régnière, 2004). Although ballooning behaviour might plausibly respond to host tree species as well, little is known about ballooning rates away from fir versus black spruce.

The simple view of a parasitism-feeding trade-off, however, neglects the substantial fitness differences seen for cohorts emerging in better or worse synchrony with budburst of the alternative hosts. Averaging across all spring cohorts suggests that, unless budworm emerge from diapause perfectly synchronous to one of its hosts' budbursts, then it does not matter much which host it is on. However, the breakdown of pre-budburst, budburst and post-budburst performance data reveals that unless larvae emerge exactly one week before balsam fir budburst, black spruce may be a similar or better host. In the field budworm emergence dates vary, although they are generally governed by ambient air temperature (Régnière, 1990; Thomas, 1976). Ignoring for the moment the complication of emergence-budburst matching (that is, averaging over all spring cohorts), this risk suggests that for budworm there may be a trade-off with spring food quality.

Similar trade-offs between host quality and exposure to parasitism among host plants have been noted previously. For example, some Lepidoptera of oak (*Quercus* spp.) that fed in the spring were feeding on much higher quality foliage but were exposed to much higher rates of parasitism (Forkner et al., 2008). Some herbivores may be less likely to feed on their hosts in the presence of their enemies. Damage to host plants of the Colorado potato beetle, *Leptinotarsa decemlineata*, as well as beetle oviposition decreased with predation risk of *Podisus maculiventris* in both greenhouse and mesocosm experiments (Hermann & Thaler, 2018). Simulated food stress of the pea aphid, *Acyrtosiphon pisum* (Harris) changed behavioral reaction to natural enemies in increasing

stress situations (Villagra et al., 2002). Prioritizing predator avoidance over food quality is not uncommon for many herbivores.

The possibility of budworm making an obvious shift to a host of lower nutritional quality to escape natural enemies further supports the paradigm of host-shifts in herbivorous insects. Host quality-parasitism trade-offs may be especially important in the context of host shifting and sympatric speciation in phytophagous insects. Models of host shifting emphasize the possibility that feeding on an alternative host may at first be just a mistake. Differences in parasitism may compensate for reduced food quality on the novel host, preventing natural selection from removing individuals susceptible to host-choice mistakes from the population. Evolution of active dietary choice could follow. *Eurosta solidaginis* Fitch, a goldenrod gall-maker experienced 76% higher survivorship across a set of sites on its novel host, *Solidago gigantea*, than its ancestral host, *Solidago altissima*, largely due to parasitism (Brown et al., 1995), although Heard et al.(2006) showed this is not necessarily a universal pattern. For a swallowtail butterfly in Alaska, *Papilio machaon* (Linnaeus), when natural enemies are present, survival is greater on their novel hosts; however, when there are no predators, survivorship and growth for the butterfly is higher on the ancestral host (Murphy, 2004).

Climate change may alter the consequences of herbivore host selection, owing to changes in synchrony between insect and host, and vulnerability to natural enemies (Pureswaran et al., 2015). This may lead to increased usage of the late bursting black spruce. It is no longer a question of host quality, but both host quality variation among hosts for natural enemies and other factors such as phenology, and the latter in particular is likely to alter with climate change. Budworm may experience overall better fitness on

black spruce not because of improved synchrony with black spruce, but decreased synchrony with balsam fir because available models suggest that emergence timing is cued by ambient temperature (Régnière, 1990; Thomas, 1976). I speculate that is possible that with climate change budworm will emerge earlier (relative to host budburst) as air temperature increases faster than soil temperature, as budburst for trees is dependent on soil temperature (Domisch et al., 2001; Lavender et al., 1973; Lopushinsky & Max, 1990). Many other studies have assessed the potential for insect-host asynchrony to increase in the presence of changing climates, as the insects emerge earlier, but little to no change occurs in their hosts' budburst (Dewar & Watt, 1992; Singer & Parmesan, 2010; van Asch & Visser, 2007).

Studies describing the tri-trophic interactions of herbivores are less abundant than those that focus on host quality or natural enemies alone. This study is the first to look at how these tri-trophic interactions may affect budworm host selection. My results help explain why this herbivore would choose a nutritionally inferior host. Additional studies examining the primary mechanisms and trade-offs of host choice and behavioral variation on different hosts could explain the pressures that shape foraging trends in this herbivore and how these trends impact the broader community structure.

LITERATURE CITED

- Baskerville, G. L., and P. Emin (1969). Rapid estimation of heat accumulation from maximum and minimum temperatures. *Ecology*, 50(3), 514-517. <https://doi.org/10.2307/1933912>
- Blais, J. R. (1952). The relationship of the spruce budworm (*Choristoneura fumiferana*, Clem.) to the flowering condition of balsam fir (*Abies balsamea* (L.) Mill.). *Canadian Journal of Zoology*, 30 (1), 1–29. <https://doi.org/10.1139/z52-001>
- Blais, J. R. (1957). Some relationships of the spruce budworm, *Choristoneura fumiferanae* (Clem.) to black spruce, *Picea mariana* (Moench) Voss. *The Forestry Chronicle*, 33, 364–372. <https://doi.org/10.5558/tfc33364-4>
- Boulanger, Y., & Arseneault, D. (2004). Spruce budworm outbreaks in eastern Quebec over the last 450 years. *Canadian Journal of Forest Research*, 34(5), 1035–1043. <https://doi.org/10.1139/x03-269>
- Brown, J. M., Abrahamson, W. G., Packer, R. A., & Way, P. A. (1995). The role of natural-enemy escape in a gallmaker host-plant shift. *Oecologia*, 104(1), 52–60. <https://doi.org/10.1007/BF00365562>
- Calvo, D., & Molina, J. M. (2005). Fecundity – body size relationship and other reproductive aspects of *Streblote panda* (Lepidoptera : Lasiocampidae). *Annals of the Entomological Society of America*, 98(2), 191–196. [https://doi.org/10.1603/0013-8746\(2005\)098\[0191:FSRAOR\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2005)098[0191:FSRAOR]2.0.CO;2)

- Carroll, A. L., & Quiring, D. T. (1994). Intratree variation in foliage development influences the foraging strategy of a caterpillar. *Ecology*, 75(7), 1978–1990. Retrieved from <http://www.jstor.org/stable/1941602>
- Chrosciewicz, Z. (1986). Foliar moisture content variations in four coniferous tree species of central Alberta. *Canadian Journal of Forest Research*, 16, 157–162. <https://doi.org/10.1139/x86-029>
- Craig, T. P., Itami, J. K., & Price, P. W. (1989). A Strong relationship between oviposition preference and larval performance in a shoot-galling sawfly. *Ecological Society of America*, 70(6), 1691–1699. <https://doi.org/10.2307/1938103>
- Dewar, R. C., & Watt, A. D. (1992). Predicted changes in the synchrony of larval emergence and budburst under climatic warming. *Oecologia*, 89, 557–559. <https://doi.org/10.3389/fpsyg.2012.00341>
- Dill, L. M., & Fraser, A. H. G. (1984). Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). *Behavioral Ecology and Sociobiology*, 16(1), 65–71. <https://doi.org/10.1007/BF00293105>
- Dodge, H. R. (1961). Parasitism of spruce budworm by *Glypta* and *Apanteles* at different Ccown heights in montana. *The Canadian Entomologist*, 93: 222-228. <https://doi.org/10.4039/Ent93222-3>
- Domisch, T., Finér, L., & Lehto, T. (2001). Effects of soil temperature on biomass and carbohydrate allocation in Scots pine (*Pinus sylvestris*) seedlings at the beginning

of the growing season. *Tree Physiology*, 21, 465–472. <https://doi.org/10.1093/treephys/21.7.465>

Donelan, S. C., & Trussell, G. C. (2015). Parental effects enhance risk tolerance and performance in offspring. *Ecology*, 96(8), 2049–2055. <https://doi.org/10.1890/14-1773.1>

Dorais, L. G., and E. Kettela. 1982. Revue, par région, des techniques d'inventaire entomologique et d'évaluation des programmes de pulvérisation à grande échelle contre la tordeuse des bourgeons de l'épinette, *Choristoneura fumiferana* (Clem.). Conseil de l'est de la tordeuse des bourgeons de l'épinette. Rapport du comité pour la standardisation des techniques entomologiques. Gouvernement du Québec, Québec, Canada.

Eveleigh, E. S., & Johns, R. C. (2014). Intratree variation in the seasonal distribution and mortality of spruce budworm (Lepidoptera: Tortricidae) from the peak to collapse of an outbreak. *Annals of the Entomological Society of America*, 107(2), 435–444. <https://doi.org/10.1603/AN13136>

Feeny, P. (1970). Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology*, 51(4), 565–581. <https://doi.org/10.2307/193403>

Forkner, R. E., Marquis, R. J., Lill, J. T., & Corff, J. Le. (2008). Timing is everything? Phenological synchrony and population variability in leaf-chewing herbivores of *Quercus*. *Ecological Entomology*, 33(2), 276–285. <https://doi.org/10.1111/j.1365-2311.2007.00976.x>

- Fuentealba, A., Pureswaran, D. S., Bauce, É., & Despland, E. (2017). How does synchrony with host plant affect the performance of an outbreaking insect defoliator? *Oecologia*, 184(4), 847–857. <https://doi.org/10.1007/s00442-017-3914-4>
- Han, E.-N., & Bauce, É. (1995). Glycerol synthesis by diapausing larvae in response to the timing of low temperature exposure, and implications for overwintering survival of the spruce budworm, *Choristoneura fumiferana*. *Journal of Insect Physiology*, 41(11), 981–985. [https://doi.org/10.1016/0022-1910\(95\)00049-Z](https://doi.org/10.1016/0022-1910(95)00049-Z)
- Han, E.-N., & Bauce, É. (1998). Timing of diapause initiation, metabolic changes and overwintering survival of the spruce budworm, *Choristoneura fumiferana*. *Ecological Entomology*, 23(2), 160–167. <https://doi.org/10.1046/j.1365-2311.1998.00111.x>
- Harvey, G. T. (1957). The occurrence and nature of diapause-free development in the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). *Canadian Journal of Zoology*, 35(4), 549–572. <https://doi.org/10.1139/z57-047>
- Haukioja, E., Pakarinen, E., Niemela, P., & Iso-Iivari, L. (1988). Crowding-triggered phenotypic responses alleviate consequences of crowding in *Epirrita autumnata* (Lep., Geometridae). *Oecologia*, 75, 549–558. <https://doi.org/10.1007/BF00776419>
- Heard, S. B., Stireman, J. O., Nason, J. D., Cox, G. H., Kolacz, C. R., & Brown, J. M. (2006). On the elusiveness of enemy-free space: Spatial, temporal, and host-plant-

- related variation in parasitoid attack rates on three gallmakers of goldenrods. *Oecologia*, 150(3), 421–434. <https://doi.org/10.1007/s00442-006-0529-6>
- Hennigar, C. R., Maclean, D. A., Quiring, D. T., & Kershaw, J. A. (2008). Differences in spruce budworm defoliation among balsam fir and black spruce. *Forest Science*, 54(2). <https://doi.org/10.1093/forestscience/54.2.158>
- Hermann, S. L., & Thaler, J. S. (2018). The effect of predator presence on the behavioral sequence from host selection to reproduction in an invulnerable stage of insect prey. *Oecologia*, 188(4), 945–952. <https://doi.org/10.1007/s00442-018-4202-7>
- Hochuli, D. F. (2001). Insect herbivory and ontogeny: How do growth and development influence feeding behaviour, morphology and host use? *Austral Ecology*, 26, 563–570. <https://doi.org/10.1046/j.1442-9993.2001.01135.x>
- Johns, R. C., & Eveleigh, E. S. (2013). Ontogeny and stand condition influence the dispersal behavior of a defoliating specialist caterpillar. *Environmental Entomology*, 42(6), 1329–1337. <https://doi.org/10.1603/EN13083>
- Johns, R. C., Quiring, D. T., & Ostaff, D. P. (2009). Sex biased intra-tree oviposition site selection and larval foraging behavior of a specialist herbivore. *Entomologia Experimentalis et Applicata*, 132(3), 264–274. <https://doi.org/10.1111/j.1570-7458.2009.00890.x>
- Johns, R. C., Quiring, D. T., Ostaff, D. P., & Bauce, É. (2010). Intra-tree variation in foliage quality drives the adaptive sex-biased foraging behaviors of a specialist herbivore. *Oecologia*, 163(4), 935–947. <https://doi.org/10.1007/s00442-010-1632-2>

- Kaitaniemi, P., Ruohomäki, K., & Haukioja, E. (1997). Consequences of defoliation on phenological interaction between *Epirrita autumnata* and its host plant, mountain birch. *Functional Ecology*, 11(2), 199–208. <https://doi.org/10.1046/j.1365-2435.1997.00063.x>
- Katovich, S.A., McCullough, D.G., Haack, R.A., 1995. Yellowheaded spruce sawfly—its ecology and management. USDA Forest Service, North Central Research Station. CTR NC-179, p. 24.
- Kessler, A., & Baldwin, I. T. (2002). *Manduca quinquemaculata*'s Optimization of intra-plant oviposition to predation, food quality, and thermal constraints. *Ecology*, 83(8), 2346–2354. <https://doi.org/10.2307/3072065>
- Lavender, D. P., Sweet, G. B., Zaerr, J. B., & Hermann, R. K. (1973). Spring shoot growth in douglas-fir may be initiated by gibberelins exported from the roots. *Science*, 182(4114), 838–839. <https://doi.org/10.1126/science.182.4114.838>
- Lawrence, R. K., Mattson, W. J., & Haack, R. A. (1997). White spruce and the spruce budworm: defining the phenological window of susceptibility. *The Canadian Entomologist*, 129(2), 291–318. <https://doi.org/10.4039/Ent129291-2>
- Lewis, F. B. (1960). Factors affecting assessment of parasitization by *Apanteles fumiferanae* Vier. and *Glypta fumiferanae* (Vier.) on Spruce Budworm Larvae. *The Canadian Entomologist*, 92(12), 881-891. [https://doi.org/10.4039/Ent92881-](https://doi.org/10.4039/Ent92881-12)

- Lopushinsky, W., & Max, T. A. (1990). Effect of soil temperature on root and shoot growth and on budburst timing in conifer seedling transplants. *New Forests*, 4(2), 107–124. <https://doi.org/10.1007/BF00119004>
- Mattson, W. J.. 1983. Spruce budworm (*Choristoneura fumiferana*) performance in relation to foliar chemistry of its host plants. In: Talerico, Robert L.; Montgomery, Michael, tech. coords. Proceedings, forest defoliator--host interactions: A comparison between gypsy moth and spruce budworms; 1983 April 5-7; New Haven, CT. Gen. Tech. Rep. NE-85. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station: 55-65.
- Mayhew, P. J. (2001). Herbivore host choice and optimal bad motherhood. *Trends in Ecology and Evolution*, 16(4), 165–167. [https://doi.org/10.1016/S0169-5347\(00\)02099-1](https://doi.org/10.1016/S0169-5347(00)02099-1)
- McMorran, A. (1965). A synthetic diet for the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). *The Canadian Entomologist*, 97(1), 58–62. <https://doi.org/10.4039/Ent9758-1>
- Miller, C. A. (1958). The measurement of spruce budworm populations and mortality during the first and second larval instars. *Canadian Journal of Zoology*, 36(3), 409–422. <https://doi.org/10.1139/z58-035>
- Miller, C. A. (1959). The interaction of spruce budworm (*Choristoneura fumiferana* (Clem.) and the parasite *Apanteles fumiferanae* Vier. *The Canadian Entomologist*, 91(8), 457–477. <https://doi.org/10.4039/entcontin142>

- Miller, C. A. (1960). The interaction of the spruce budworm, *Choristoneura fumiferana* (Clem.), and the parasite *Glypta fumiferanae* (Vier.). *The Canadian Entomologist*, 92(11), 839–850. <https://doi.org/10.4039/Ent92839-11>
- Miller, C. A., & Kettela, E. G. (1972). An additional note on sampling overwintering spruce budworm larvae. Fredericton, NB. Information Report M-X-34. 11 p.
- Miller, C.A., Kettela, E.G., McDougall, G.A. (1971) A sampling technique for overwintering spruce budworm and its applicability to population surveys. Fredericton, NB. Information Report M-X-25. 13 p.
- Morris, R. F. (1963). The dynamics of epidemic spruce budworm populations. *Entomological Society of Canada*, 95, 1-12. <https://doi.org/10.4039/entm9531fv>
- Murphy, S. M. (2004). Enemy-free space maintains swallowtail butterfly host shift. *Proceedings of the National Academy of Sciences*, 101(52), 18048–18052. <https://doi.org/10.1073/pnas.0406490102>
- Murphy, S. M., & Loewy, K. J. (2015). Trade-offs in host choice of an herbivorous insect based on parasitism and larval performance. *Oecologia*, 179(3), 741–751. <https://doi.org/10.1007/s00442-015-3373-8>
- Nealis, V. G., & Régnière, J. (2004). Insect-host relationships influencing disturbance by the spruce budworm in a boreal mixedwood forest. *Canadian Journal of Forest Research*, 34(9), 1870–1882. <https://doi.org/10.1139/x04-061>

- Nealis, V. G., & Régnière, J. (2016). Why western spruce budworms travel so far for the winter. *Ecological Entomology*, 41(5), 633–641.
<https://doi.org/10.1111/een.12336>
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & Team, R. C. (2017). nlme: Linear and Nonlinear Mixed Effects Models_. R package version 3.1-131. Retrieved from <https://cran.r-project.org/package=nlme%3E>
- Price, P. W., Roininen, H., & Tahvanainen, J. (1987). Plant age and attack by the bud galler , *Euura mucronata*. *Oecologia*, 73(3), 334–337.
<https://doi.org/10.1007/BF00385248>
- Pureswaran, D. S., De Grandpré, L., Pare, D., Taylor, A., Barrette, M., Morin, H., Régnière, J., Kneeshaw, D. (2015). Climate-induced changes in host tree-insect phenology may drive ecological state-shift in boreal forest. *Ecology*, 96(6), 1480–1491. <https://doi.org/10.1890/07-1861.1>
- Régnière, J. (1990). Diapause termination and changes in thermal responses during postdiapause development in larvae of the spruce budworm, *Choristoneura fumiferana*. *Journal of Insect Physiology*, 36(10), 727–735.
[https://doi.org/10.1016/0022-1910\(90\)90046-I](https://doi.org/10.1016/0022-1910(90)90046-I)
- Régnière, J., & Duval, P. (1998). Overwintering mortality of spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae), populations under field conditions. *The Canadian Entomologist*, 130(1), 13–26.
<https://doi.org/10.4039/Ent13013-1>

- Régnière, J., & Nealis, V. G. (2007). Ecological mechanisms of population change during outbreaks of the spruce budworm. *Ecological Entomology*, 32(5), 461–477.
<https://doi.org/10.1111/j.1365-2311.2007.00888.x>
- Royama, T. (1984). Population dynamics of the spruce budworm *Choristoneura fumiferana*. *Ecological Society of America*, 54(4), 429–462.
<https://doi.org/10.2307/1942595>
- Schwartzberg, E. G., Jamieson, M. A., Raffa, K. F., Reich, P. B., Montgomery, R. A., & Lindroth, R. L. (2014). Simulated climate warming alters phenological synchrony between an outbreak insect herbivore and host trees. *Oecologia*, 175(3), 1041–1049. <https://doi.org/10.1007/s00442-014-2960-4>
- Seehausen, M. L., Labrecque, M., Martel, V., Régnière, J., Mansour, A., & Smith, S. M. (2016). Reproductive biology and behavior of *Tranosema rostrale* (Hymenoptera: Ichneumonidae), a parasitoid of low-density spruce budworm (Lepidoptera: Tortricidae) populations. *Journal of Insect Behavior*, 29(5), 500–514.
<https://doi.org/10.1007/s10905-016-9576-y>
- Singer, M. C., & Parmesan, C. (2010). Phenological asynchrony between herbivorous insects and their hosts: Signal of climate change or pre-existing adaptive strategy? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1555), 3161–3176. <https://doi.org/10.1098/rstb.2010.0144>
- Sower, L. L., & Mitchell, R. G. (1987). Host-tree selection by western pine shoot borer (Lepidoptera: Olethreutidae) in ponderosa pine plantations. *Environ. Entomol.* 16(5), 1145–1147. <https://doi.org/10.1093/ee/16.5.1145>

- Thomas, A. W. (1976). The effects of temperature on the emergence of second-instar spruce budworm larvae. Fredericton, NB. Information Report M-X-60. 8 p.
- Thomas, A. W., Borland, S. A., & Greenbank, D. O. (1980). Field fecundity of the spruce budworm (Lepidoptera : Tortricidae) as determined from regression relationships between egg complement, fore wing length, and body weight. . *Can. J. Zool.*, 58, 1608-161. <https://doi.org/10.1139/z80-220>
- Trier, T. M., & Mattson, W. J. (1997). Needle mining by the spruce budworm provides sustenance in the midst of privation. *Oikos*, 79, 241–246.
<http://doi.org/10.2307/3546009>
- Tuomi, J., Niemela, P., Jussila, I., Vuorisalo, T., & Jormalainen, V. (1989). Delayed budbreak : A defensive response of mountain birch to early-season defoliation. *Oikos*, 54(1), 87–91. <https://doi.org/10.2307/3565900>
- van Asch, M., & Visser, M. E. (2007). Phenology of forest caterpillars and their host trees: the importance of synchrony. *Annual Review of Entomology*, 52(1), 37–55.
<https://doi.org/10.1146/annurev.ento.52.110405.091418>
- Villagra, C. A., Ramírez, C. C., & Niemeyer, H. M. (2002). Antipredator responses of aphids to parasitoids change as a function of aphid physiological state. *Animal Behaviour*, 64(5), 677–683. <https://doi.org/10.1006/anbe.2002.4015>
- Vinson, S. B. (1976). Host selection by insect parasitoids. *Annual Review of Entomology*, 21(1), 109–133.
<https://doi.org/10.1146/annurev.en.21.010176.000545>

Volney, W. J. A., & Cerezke, H. F. (1992). The phenology of white spruce and the spruce budworm in northern Alberta. *Canadian Journal of Forest Research*, 22(2), 198-205. <https://doi.org/10.1139/x92-026>

Table 1. Site characteristics.

Experiment	Site	Year	Lat./Long.	Elevation (m)	No. of trees	Balsam fir		Black spruce		Spacing (m)
						Mean DBH (cm)	Count	Mean DBH (cm)	Count	
Overwintering mortality and distribution	Charlo	2017	N 47°59'24", W 66°20'03"	42	10	8.6	27 ±5	7.2	22 ±5	5
	Miramichi	2018	N 47°00'34", W 65°27'54", N 46°03.300', W 66°31.364'	33	20	5.5	5 ±0.5	5.1	2 ±0.7	5
Larval feeding performance	Noonan	2016 2017	N 46°02.006, W 66°28.277	77	15	9.3	5	9.9	5	5

Table 2. Linear mixed effects model of density of moths on individual trees from 2017 and 2018 overwintering distribution assessment. (*) indicates p-value is less than 0.05, (**) indicates p-value is less than 0.01, (***) indicates p-value is less than 0.001.

Year	Effect	numDF	denDF	F value	Pr(>F)
2017	Species	1	37	0.79	0.38
	Crown level	1	37	6.38	0.016*
2018	Species	1	77	0.83	0.37
	Crown level	1	77	6.83	0.011*

Table 3. Linear mixed effects model of overwintering survivorship and parasitism of balsam fir and black spruce from 2017 and 2018. (*) indicates p-value is less than 0.05, (**) indicates p-value is less than 0.01, (***) indicates p-value is less than 0.001.

	Year	Effect	numDF	denDF	F value	Pr(>F)
Total	2017	Species	1	37	0.63	0.43
		Crown level	1	37	2.63	0.11
Mortality	2018	Species	1	53	0.062	0.80
		Crown level	1	53	0.29	0.59
Parasitism	2017	Species	1	37	6.38	0.016*
		Crown level	1	37	13.2	0.0008***
	2018	Species	1	53	2.54	0.11
		Crown level	1	53	0.30	0.58

Table 4. Linear mixed effects model of species breakdown of parasitism by the two most abundant parasitoids in 2017. (*) indicates p-value is less than 0.05, (**) indicates p-value is less than 0.01, (***) indicates p-value is less than 0.001.

	Year	Effect	numDF	denDF	F value	Pr(>F)
<i>Glypta</i>	2017	Species	1	28	1.50	0.23
<i>fumiferanae</i>		Crown level	1	28	14.26	0.0008***
<i>Apanteles</i>	2017	Species	1	28	3.18	0.086
<i>fumiferanae</i>		Crown level	1	28	9.16	0.0053***

Table 5. Linear mixed effects model of spring survival and average female wing length from 2016 and 2017(linear mixed effects model). (*) indicates p-value is less than 0.05, (**) indicates p-value is less than 0.01, (***) indicates p-value is less than 0.001.

	Year	Effect	numDF	denDF	F value	Pr(>F)
Survival	2016	Species	1	173	14.5	0.0002***
		Cohort	5	173	3.57	0.0043***
	2017	Species	1	412	42.5	<.0001***
		Cohort	6	412	5.02	<.0001**
Wing length	2016	Species	1	31	0.36	0.55
		Cohort	5	31	0.91	0.49
	2017	Species	1	202	3.28	0.072
		Cohort	6	202	5.32	<.0001***

Table 6. Linear mixed effects model of fitness per second-instar larva as the product of survivorship and per-survivor fecundity of all combinations of years from the overwintering distribution and spring emergence experiments. (*) indicates p-value is less than 0.05, (**) indicates p-value is less than 0.01, (***) indicates p-value is less than 0.001.

Year	Effect	numDF	denDF	F value	Pr(>F)
2016 by 2017	Species	1	31	1.61	0.21
	Cohort	5	31	0.59	0.70
2016 by 2018	Species	1	31	0.25	0.62
	Cohort	5	31	0.56	0.73
2017 by 2017	Species	1	206	2.62	0.11
	Cohort	6	206	3.87	0.0504
2017 by 2018	Species	1	206	0.19	0.66
	Cohort	6	206	3.87	0.0505

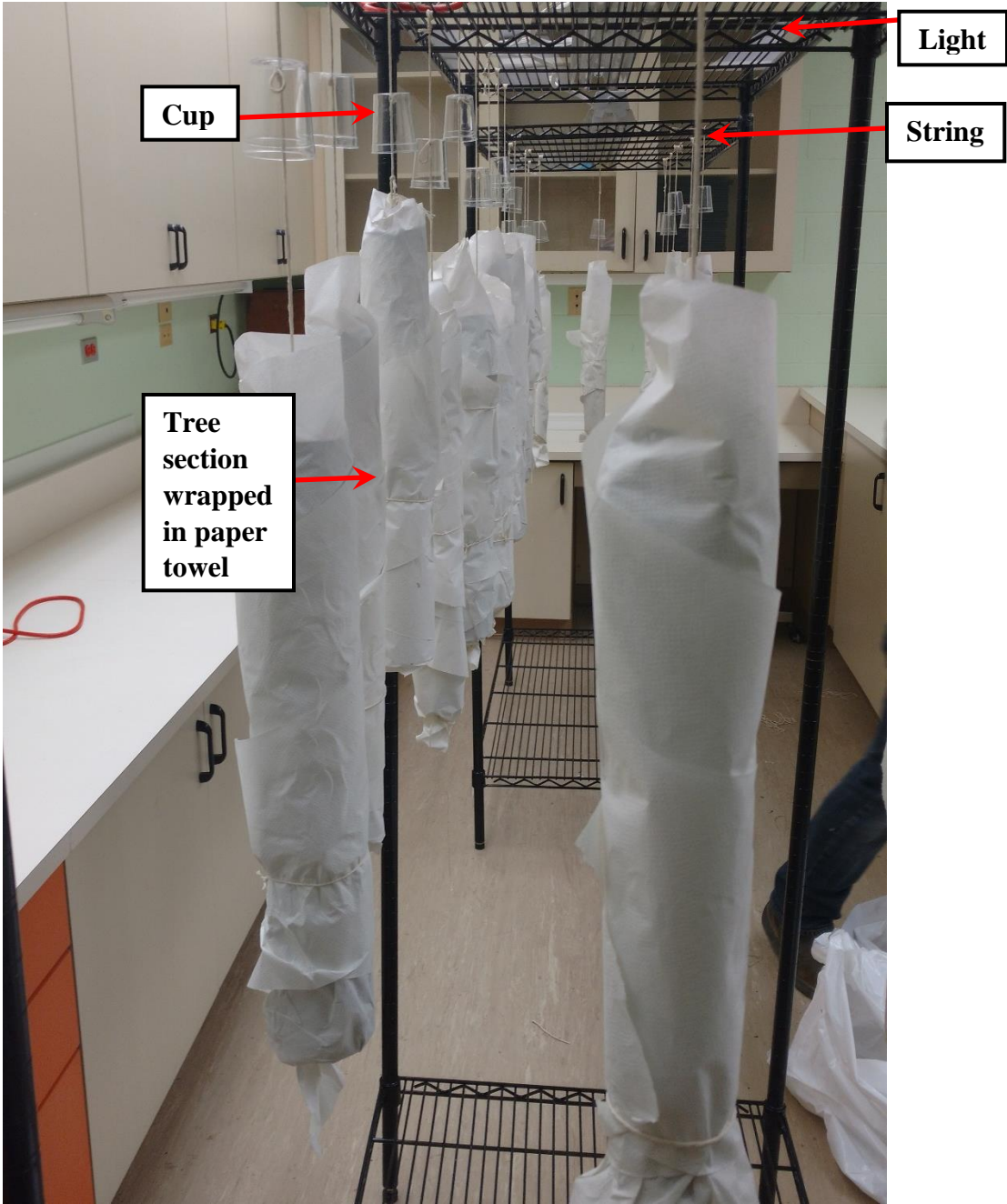


Figure 1. Setup of second-instar larval emergence traps for spruce budworm.

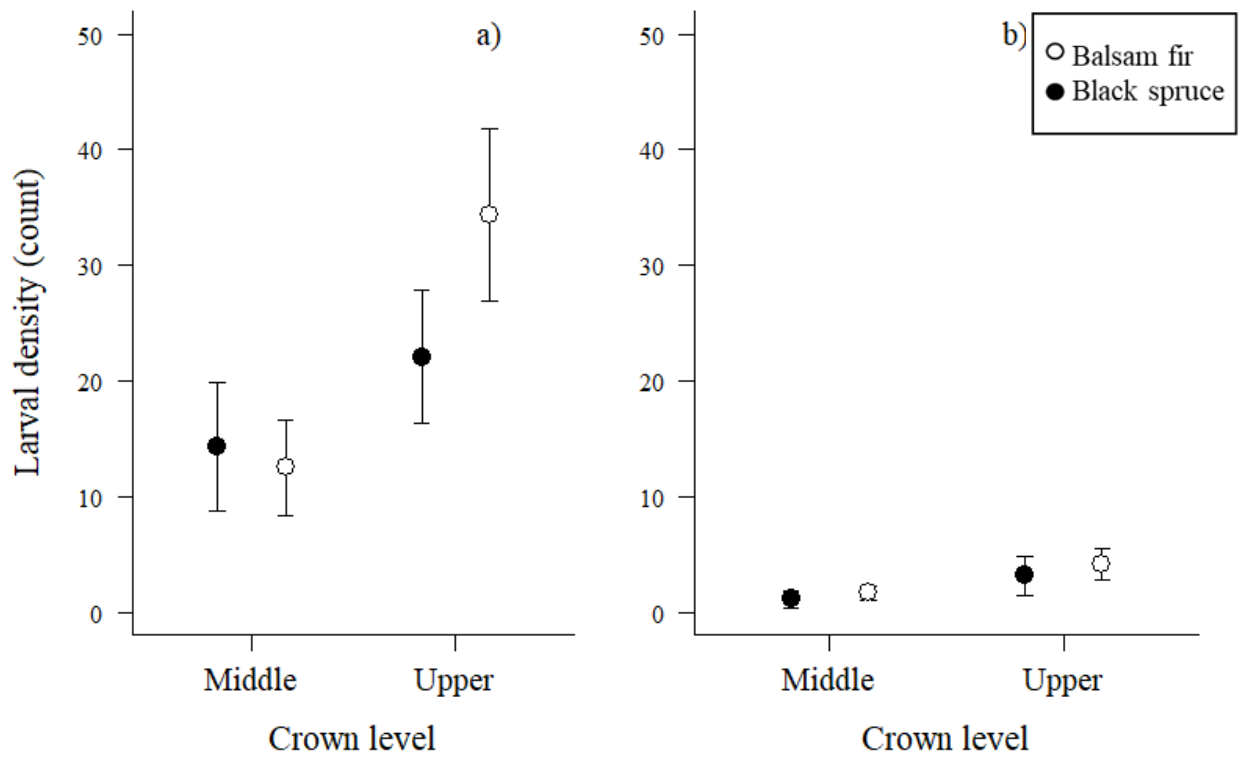


Figure 2. Total number of overwintering survivors combined with budworm larvae that died prior to emergence (extracted by a sodium hydroxide rinse) from the overwintering distribution assessment in a) 2017 and b) 2018.

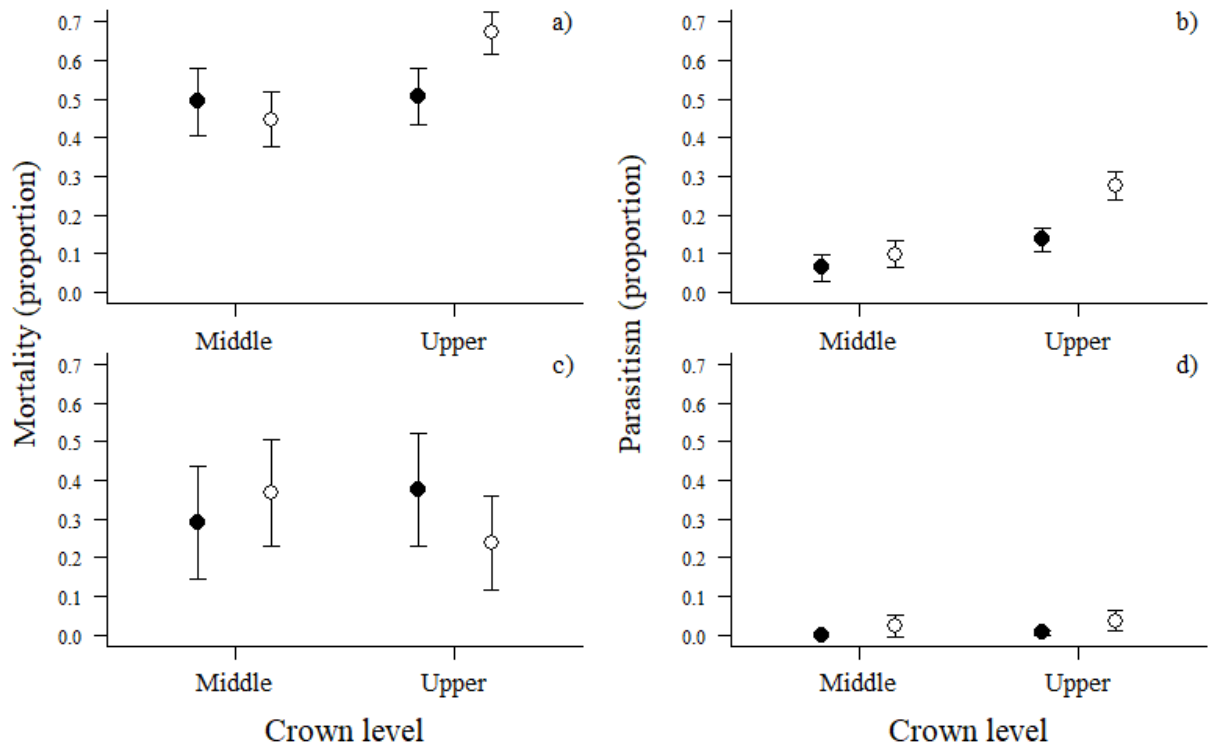


Figure 3. Proportion of mortality (a) 2017 and (c) 2018) and parasitism (b) 2017 and (d) 2018) between balsam fir (○) and black spruce (●) in different parts of the tree crown.

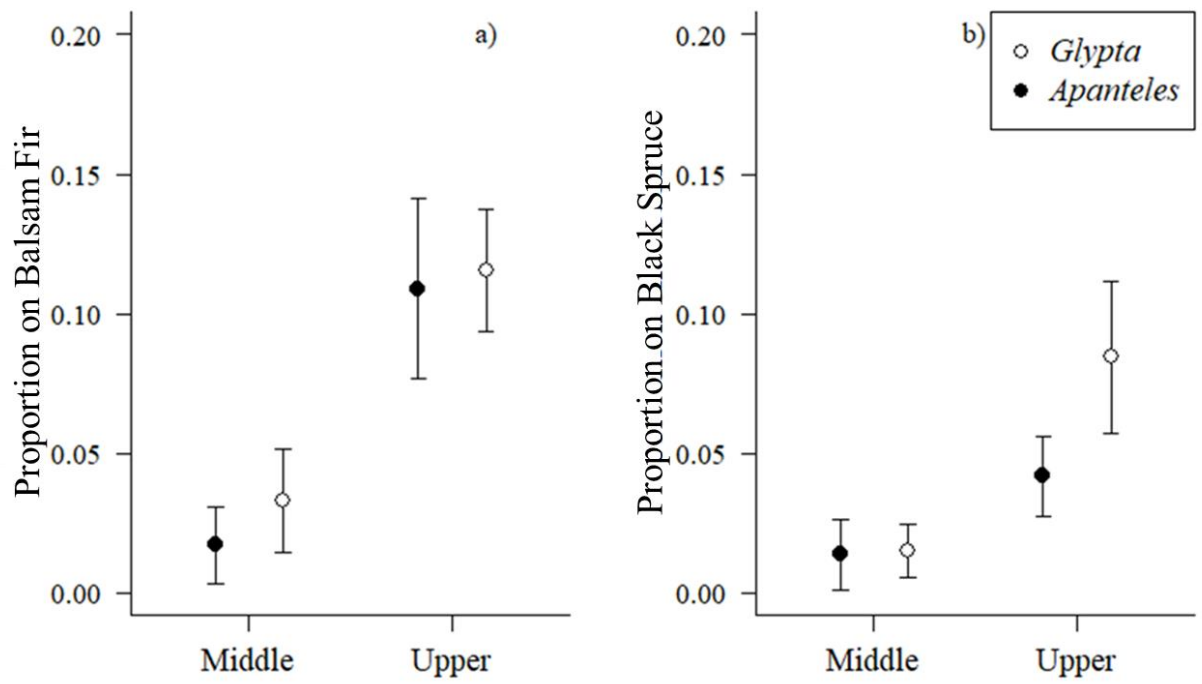


Figure 4. Proportion of parasitism on the two hosts, and crown level canopy positions by specialist parasitism in 2017.

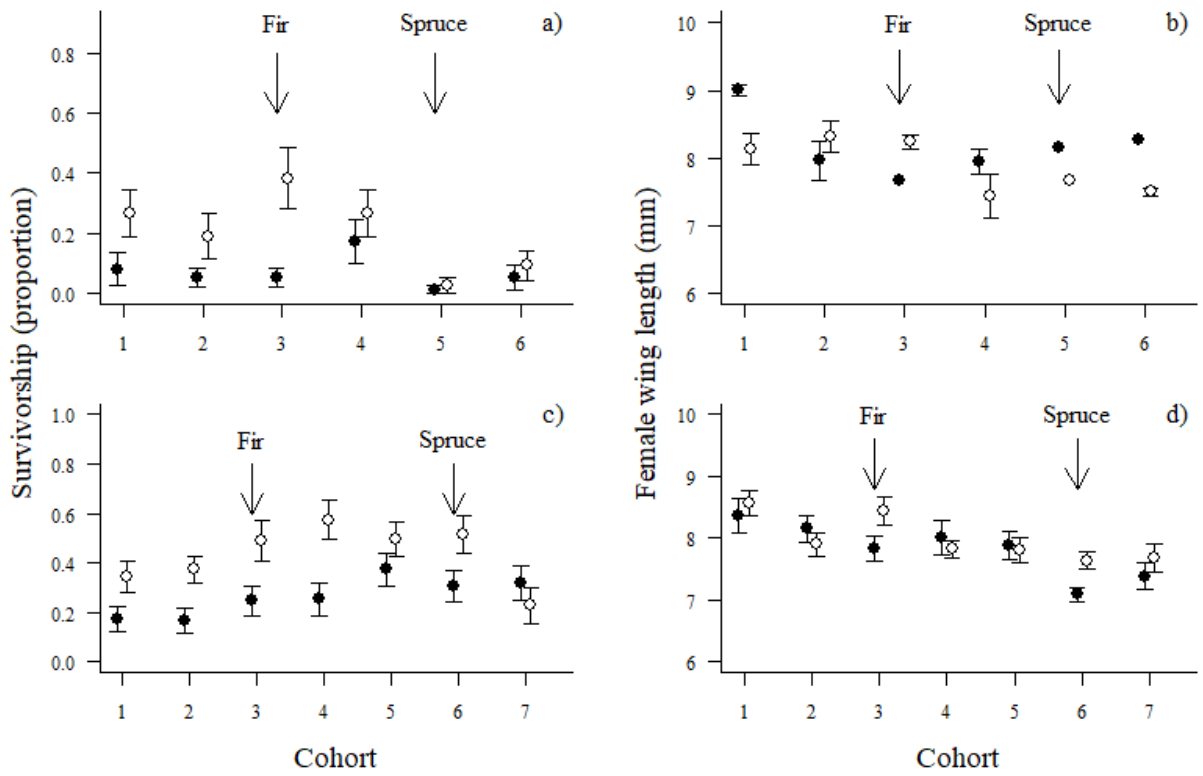


Figure 5. Proportion of survivorship (a) 2016 and (c) 2017) and female moth wing length (b) 2016 and (d) 2017) for budworm between balsam fir (○) and black spruce (●). Arrows indicate budburst for the corresponding tree species.

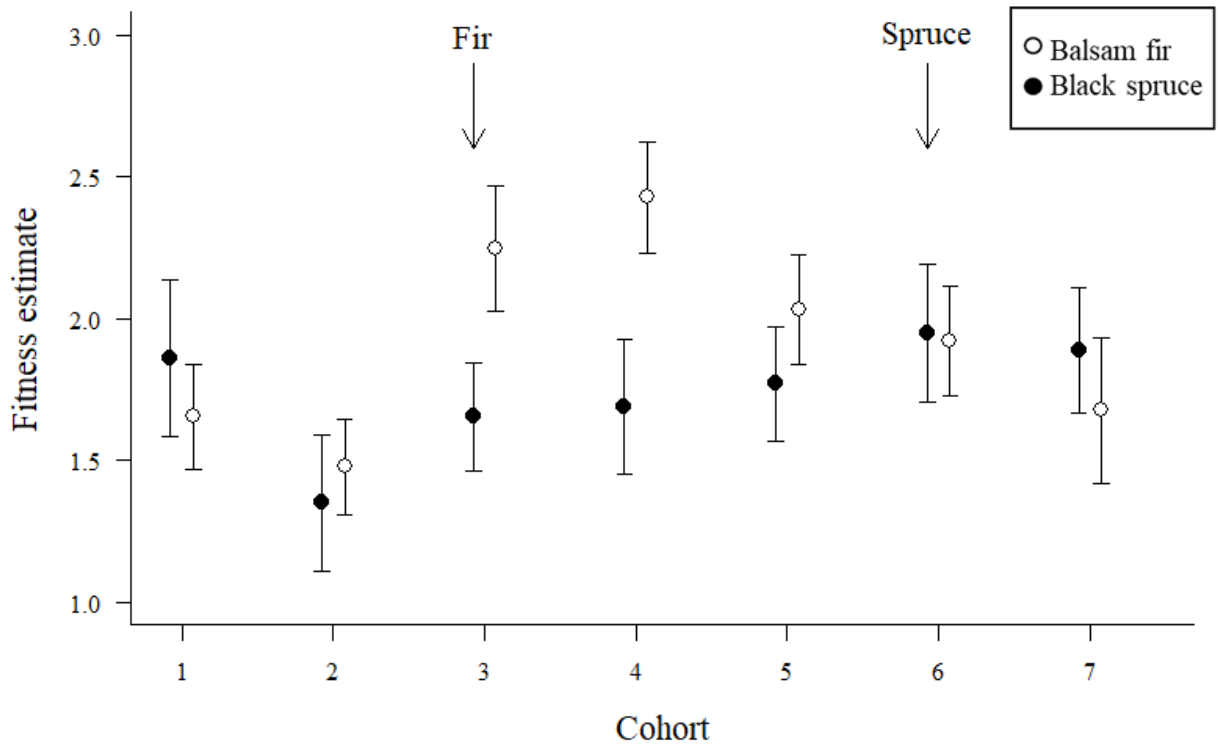


Figure 6. Budworm fitness estimate from the 2017 early and late spring emergence experiment and 2017 overwintering mortality experiment. Arrows indicate budburst for the corresponding tree species.

CHAPTER 3- GENERAL CONCLUSION

LAUREN STEAD

Department of Biology, University of New Brunswick, PO Box 4400, Fredericton, New Brunswick, E3B 5A3

My thesis provides some explanation as to why budworm would choose a previously assumed inferior host. Moreover, my study suggests a more complicated dynamic than has been described previously in studies focused on bottom-up effects of balsam fir versus black spruce. Budworm may face opposing selective pressures from bottom-up and top-down factors when selecting a host tree. Increased asynchrony owing to climate change may alter host suitability and increase herbivory in northern black spruce dominant forests (Pureswaran et al., 2015).

Top-down pressure associated with parasitoids appears to be the primary reason why budworm would benefit from overwintering on black spruce. Overwintering on balsam fir exposes budworm to natural enemies, *A. fumiferanae* and *G. fumiferanae*, which attack larvae prior to entering diapause. These two parasitoids have a bias for the upper crown of balsam fir (Dodge, 1961; Miller, 1959, 1960). This is likely due to budworm evolving primarily with balsam fir and white spruce, leading to parasitoids seeking budworm feeding on those species in comparison to black spruce. Although I was able to account for a significant amount of mortality in the overwintering distribution and mortality experiment, it is possible that some budworm were never retrieved. Regnière and Duval (1998) found that actual branch dissection was more effective in recovering budworm than the sodium hydroxide extraction technique. Budworm can fail to emerge in this forced emerged emergences technique due to poor environmental conditions or

initially being a weak individual (Régnière & Duval, 1998).

Spring-time feeding on balsam fir had higher larval survival consistently across the phenological window, except after black spruce buds burst. Similarly, Fuentealba et al. (2017) showed that budworm on balsam fir trended towards higher survival than those on black spruce, so I questioned why budworm larvae would even select black spruce as a host, if balsam fir was available.

Optimizing timing of emergence is only one ecological challenge for budworm. There is also the matter of host selection: larvae may occur on either spruce or fir, and because they move rather little between spring emergence and the initiation of feeding, their spring performance on a host is tied to their overwinter survival on that host. Budworm risk exposing their eggs to higher parasitism if they choose to lay on balsam fir, but if those eggs survive they have a superior feeding host, and the opposite occurs for budworm that choose to lay their eggs on black spruce. Assessing trade-offs in early versus late spring emergence and examining larval overwintering distribution among different host trees tell us two very different stories. Studies looking at spring feeding of budworm have only looked at the bottom-up effects of the host-plant interaction, taking into consideration variables such as foliage chemistry and quality (Fuentealba et al., 2017; Lawrence et al., 1997). I provide some additional insight on the top-down effects. Overwintering on balsam fir puts budworm larvae at greater risk of parasitism. With our fitness estimate, combining both experiments, it seems that there is no real difference in host selection for the female moths to lay their eggs. This might depend on whether the females can predict when their offspring are going to emerge in spring. If they can, then they can match timing to budburst of a host and achieve superior performance on fir.

However, they presumably cannot, in which case they will do just as well, if not better, on black spruce. As a result, a female may bet-hedge by selecting both hosts, although this has not been widely studied in budworm.

Budworm, like many organisms, may experience changes in the presence of climate change (Pureswaran et al., 2015). Budworm larvae emerge after an accumulated ambient air temperature (Miller et al., 1971), whereas trees flush the new vegetation based on soil temperature (Lopushinsky & Max, 1990). Since budworm emergence and its hosts budbreak don't use the same cues in the same manner, we may see one of several potential outcomes that could arise in the presence of climate change. First, warming temperatures could change synchrony of budburst of black spruce to better align with budworm emergence making black spruce the preferred host (Fuentelba et al., 2017). Most literature suggests that climate change will advance insect phenology more than the hosts. This outcome suggests that synchrony with its host will not be aligned with budworm emergence making budworm generally less fit and possibly reduce outbreaks. Many studies suggest that the advanced phenology will be more extreme in insects rather than their host trees. However, in a simulated warming experiment, tree phenology of white birch (*Betula papyrifera* Marshall) and trembling aspen (*Populus tremuloides* Michx.) advanced more than the forest tent caterpillar (*Malacosoma disstria* Hübner) feeding on these hosts (Schwartzberg et al., 2014). Given that budworm frequently undergoes immense variability in its population dynamics, outbreaking populations every 30-40 years may allow selection to favour budworm that are synchronous to its host. If climate changes, then selection or heritability may act strongly to change budworm emergence timing, since the fitness differences I have suggested above are strong selection differentials.

It is not uncommon for organisms to face trade-offs between a good quality host and avoiding natural enemies. When feeding on sacred datura (*Datura wrightii*), tobacco hornworm (*Manduca sexta*) had a higher number of eggs hatch in comparison to a recently discovered host *Proboscidea parviflora*. However, those larvae on datura experienced much higher rates of predation and parasitism (Murphy & Loewy, 2015). Although insect herbivores are an excellent system in which to study this kind of trade-off, similar trade-offs are seen in a variety of taxa.

LITERATURE CITED

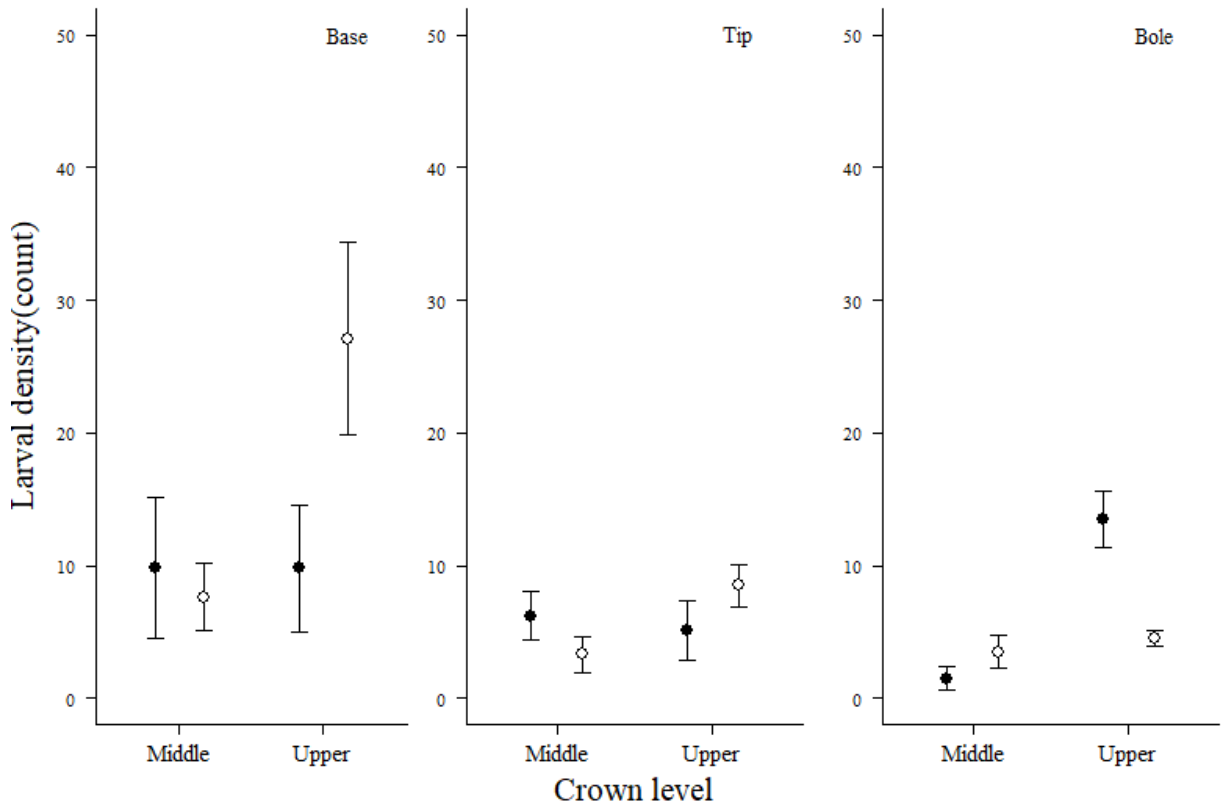
- Dodge, H. R. (1961). Parasitism of Spruce Budworm by *Glypta* and *Apanteles* at Different Crown Heights in Montana. *The Canadian Entomologist*, 93: 222-228. <https://doi.org/10.4039/Ent93222-3>
- Fuentealba, A., Pureswaran, D. S., Bauce, É., & Despland, E. (2017). How does synchrony with host plant affect the performance of an outbreaking insect defoliator? *Oecologia*, 184(4), 847–857. <https://doi.org/10.1007/s00442-017-3914-4>
- Lawrence, R. K., Mattson, W. J., & Haack, R. A. (1997). White Spruce and the Spruce Budworm: Defining the Phenological Window of Susceptibility. *The Canadian Entomologist*, 129(2), 291–318. <https://doi.org/10.4039/Ent129291-2>
- Lopushinsky, W., & Max, T. A. (1990). Effect of soil temperature on root and shoot growth and on budburst timing in conifer seedling transplants. *New Forests*, 4(2), 107–124. <https://doi.org/10.1007/BF00119004>
- Miller, C. A. (1959). The interaction of spruce budworm (*Choristoneura fumiferana* (Clem.) and the Parasite *Apanteles fumiferanae* Vier. *The Canadian Entomologist*, 91(8), 457–477. <https://doi.org/10.4039/entcontin142>
- Miller, C. A. (1960). The Interaction of the Spruce Budworm, *Choristoneura fumiferana* (Clem.), and the Parasite *Glypta fumiferanae* (Vier.). *The Canadian Entomologist*, 92(11), 839–850. <https://doi.org/10.4039/Ent92839-11>

- Miller, C.A., Kettela, E.G., McDougall, G.A. (1971) A sampling technique for overwintering spruce budworm and its applicability to population surveys. Fredericton, NB. Information Report M-X-25. 11 p.
- Murphy, S. M., & Loewy, K. J. (2015). Trade-offs in host choice of an herbivorous insect based on parasitism and larval performance. *Oecologia*, 179(3), 741–751. <https://doi.org/10.1007/s00442-015-3373-8>
- Pureswaran, D. S., De Grandpré, L., Pare, D., Taylor, A., Barrette, M., Morin, H., ... Kneeshaw, D. (2015). Climate-induced changes in host tree-insect phenology may drive ecological state-shift in boreal forest. *Ecology*, 96(6), 1480–1491. <https://doi.org/10.1890/07-1861.1>
- Régnière, J., & Duval, P. (1998). Overwintering mortality of spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae), populations under field conditions. *The Canadian Entomologist*, 130, 13–26. <https://doi.org/104039/Ent131013-1>
- Schwartzberg, E. G., Jamieson, M. A., Raffa, K. F., Reich, P. B., Montgomery, R. A., & Lindroth, R. L. (2014). Simulated climate warming alters phenological synchrony between an outbreak insect herbivore and host trees. *Oecologia*, 175(3), 1041–1049. <https://doi.org/10.1007/s00442-014-2960-4>

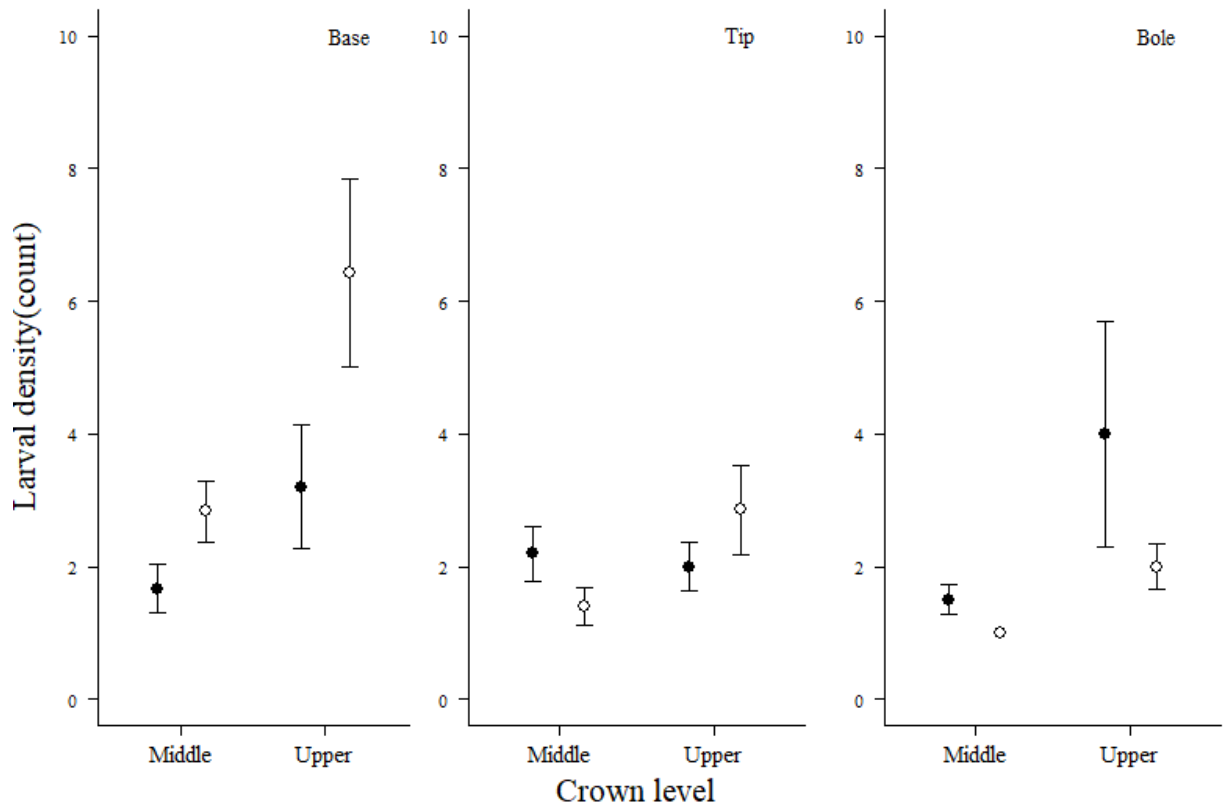
APPENDIX 1

For the overwintering distribution and mortality experiment, I collected many sections of the tree to get a complete understanding of where budworm were spending their time in diapause. The following figures show where those budworm were on their host trees, and where they were being attacked by parasitoids.

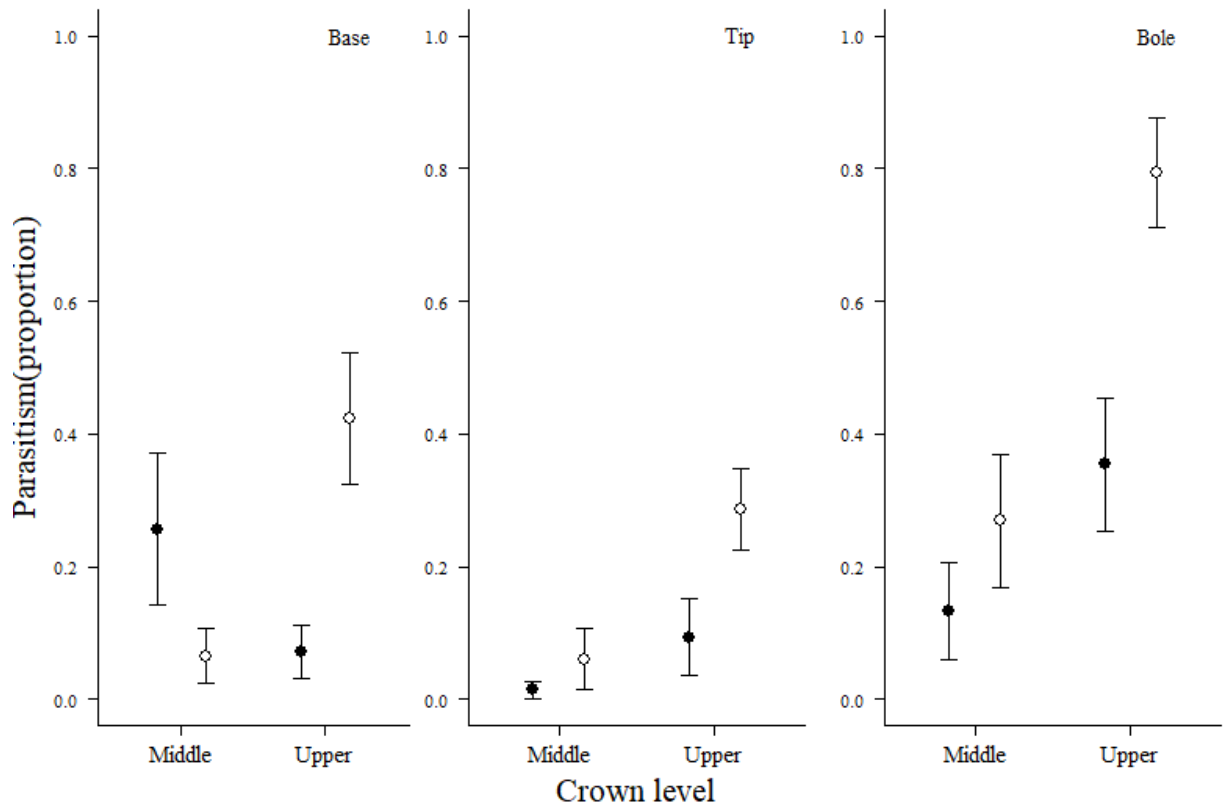
Appendix 1.1 Tree crown dissection of budworm densities from 2017 between balsam fir (○) and black spruce (●).



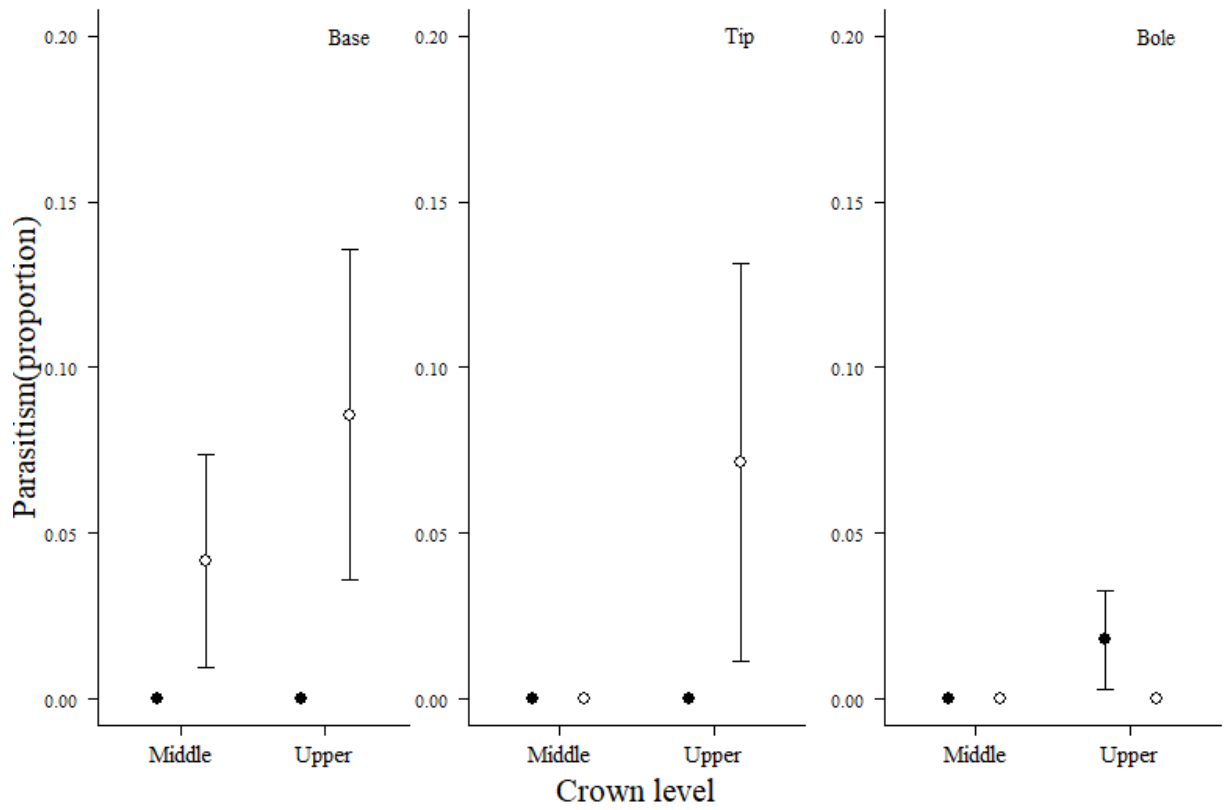
Appendix 1.2 Tree crown dissection of budworm densities from 2018 between balsam fir (○) and black spruce (●).



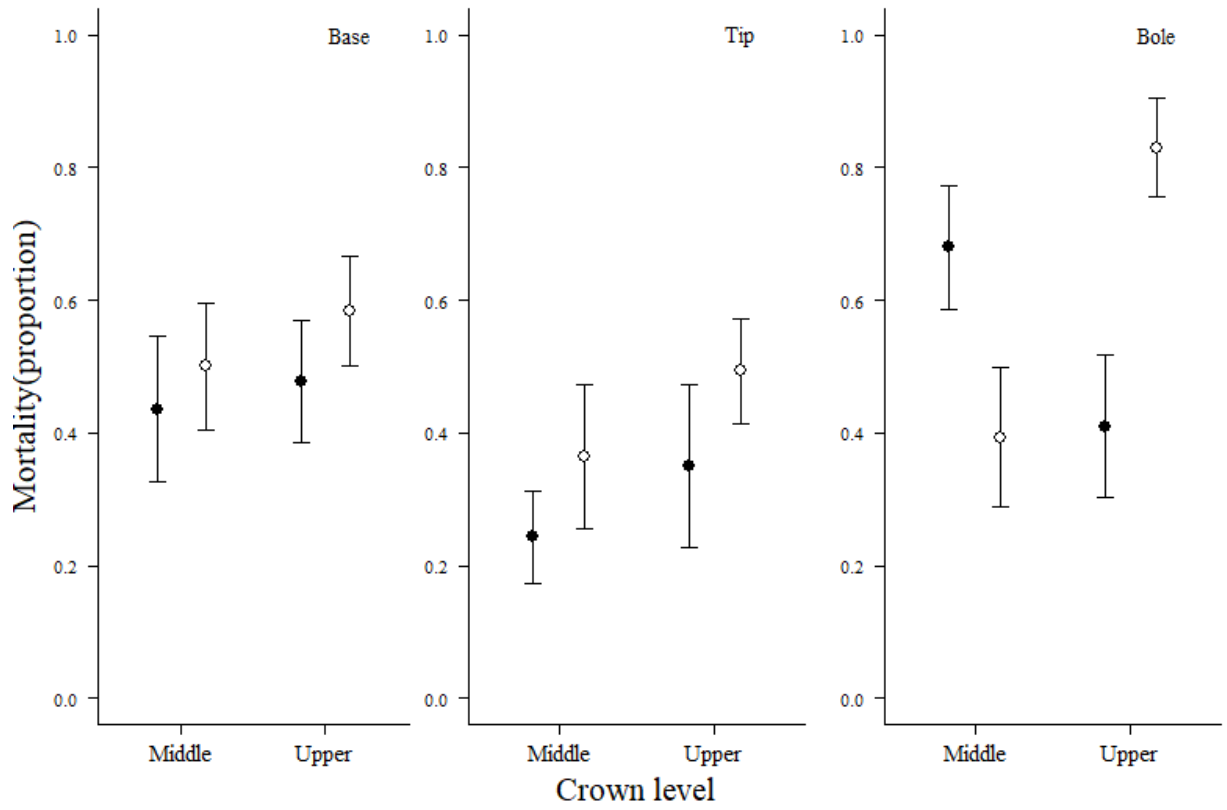
Appendix 1.3 Tree crown dissection of budworm parasitoid attack from 2017 between balsam fir (○) and black spruce (●).



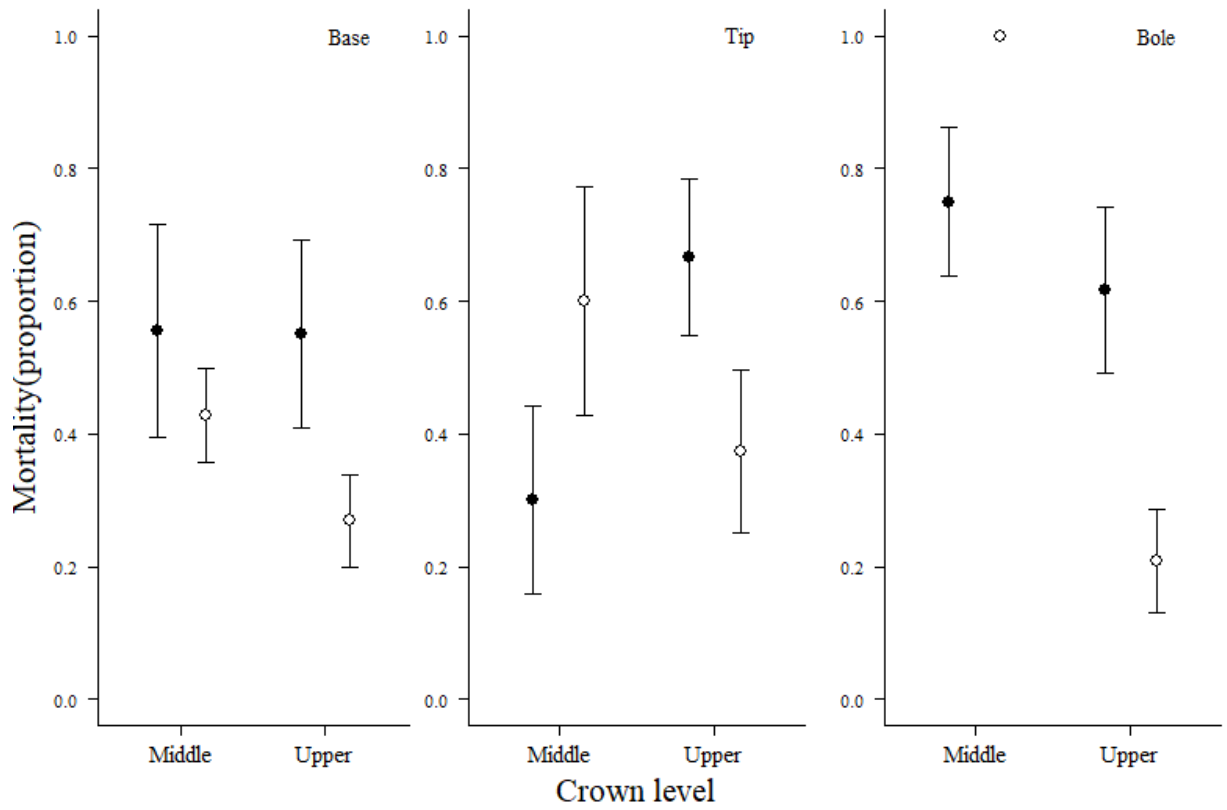
Appendix 1.4 Tree crown dissection of budworm parasitoid attack from 2018 between balsam fir (○) and black spruce (●).



Appendix 1.5 Tree crown dissection of total budworm mortality from 2017 between balsam fir (○) and black spruce (●).

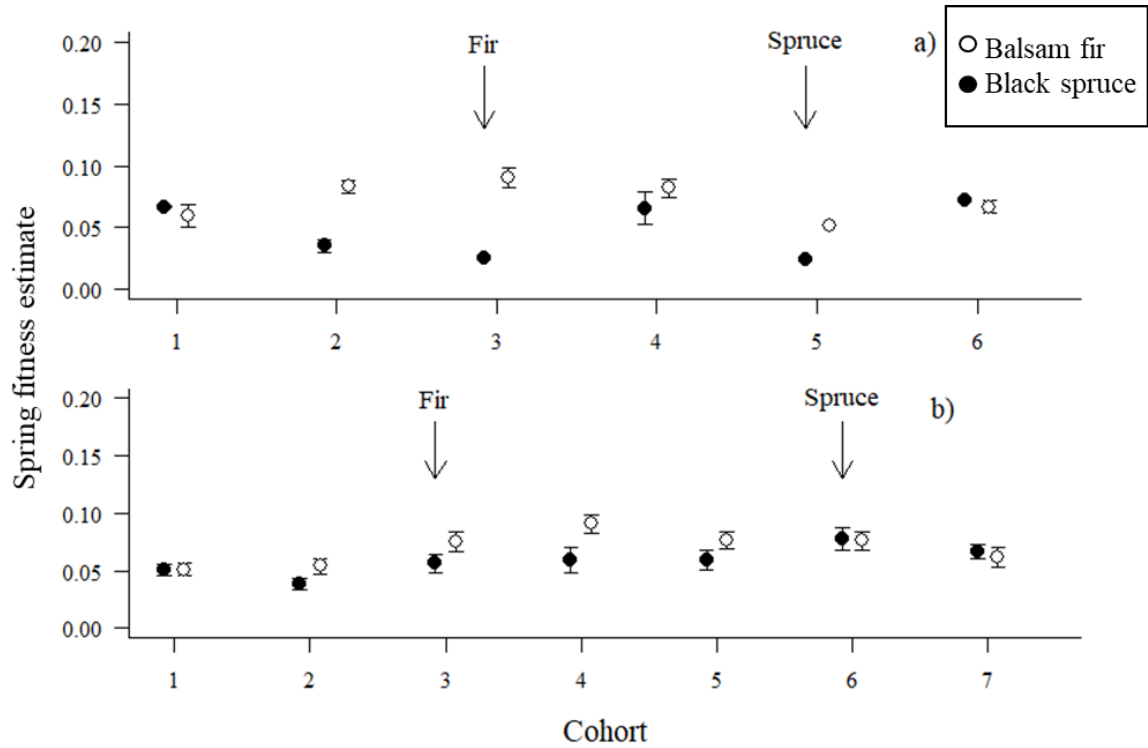


Appendix 1.6 Tree crown dissection from total budworm mortality from 2018 between balsam fir (○) and black spruce (●).



APPENDIX 2

Appendix 2.1 Spring budworm fitness calculation (survival for each cohort divided by average wing length per branch) for a) 2016 and b) 2017.



CURRICULUM VITAE

Candidate's full name:

Lauren Elizabeth Fraser Stead

Universities attended:

University of New Brunswick
2011-2015

Bachelor of Science in Environment and
Natural Resources

University of New Brunswick
2016-2019

Masters of Science in Biology

Conference Presentations:

L. Stead (July 2018) Eat well or avoid being eaten?: Life-history trade-offs in host choice of a specialist folivore. Canadian Society for Ecology and Evolution Annual General Meeting.