# Western balsam bark beetle, *Dryocoetes confusus* Swaine (Coleoptera: Curculionidae: Scolytinae), *in situ* development and seasonal flight periodicity in southern British Columbia

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## ABSTRACT

*In situ* development and seasonal flight periodicity of the western balsam bark beetle, *Dryocoetes confusus* Swaine, was observed in subalpine fir, *Abies lasiocarpa* (Hook) Nutt. stands in southern British Columbia for three years between 1998 and 2002. This study shows developmental differences of western balsam bark beetle in downed and in standing, live subalpine fir. Larval development was slower in the downed trees. Recorded daily minimum phloem temperatures were significantly lower for downed trees than for standing trees during periods of beetle development and flight. There were no significant differences in the recorded daily maximum phloem temperatures between standing and downed trees until late summer, when downed trees saw cooler daily maximum phloem temperatures. This cooler host habitat would provide fewer degree days for insect development. Three distinct larval instars were identified by head capsule measurement. There were two flights per season, the first and major flight occurring from late June to late July, and the other smaller flight occurring in late August. A combination of minimum daily phloem temperatures reaching 5° C and maximum daily phloem temperatures approaching 20° C appeared to trigger the onset of beetle flight, with flight initiated earlier in the season at lower elevations.

**Key words**: development, instar determination, subcortical temperature

## INTRODUCTION

The western balsam bark beetle, *Dryocoetes confusus* Swaine (Coleoptera: Curculionidae: Scolytinae), is the most destructive insect pest of mature and over-mature subalpine fir, *Abies lasiocarpa* (Hook.) Nutt. in British Columbia (B.C.) (Garbutt 1992). Western balsam bark beetle is found throughout the range of subalpine fir and is the dominant successional force in high-elevation ecosystems of the Engelmann Spruce–Subalpine Fir zone (ESSF) (Stock *et al.* 1994; Maclauchlan 2016), which include dry, moist, and wet subzones (Meidinger and Pojar 1991). Tree mortality from this beetle is first noticed in stands approaching 70–90 years of age (Maclauchlan 2001) and, as stands age, the aggregated pattern of attack by western balsam bark beetle describes the small-scale gap dynamic process, which over time releases the next generation of subalpine fir (Stock *et al.* 1994). Subalpine fir is susceptible to a wide variety of other disturbance agents, including two-year-cycle budworm, *Choristoneura biennis* Freeman, various root and butt rots, stem rots, animal damage and windthrow (Alexander 1987; Unger 1995; Parish and Antos 2002). Fire is relatively rare in the wetter ESSF subzones (Anon. 1995), often seen as small, localized events. Despite these other disturbances, western balsam bark beetle is one of the primary drivers of succession in both the ESSF and other subalpine fir-dominated ecosystems throughout B.C. (Maclauchlan *et al.* 2003; Maclauchlan 2016).

Western balsam bark beetle selectively kills small groups of subalpine fir at a relatively low, but constant, level each year in infested stands (Stock *et al.* 1994; Unger

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and Stewart 1992; McMillin *et al.* 2003). Recently killed, red trees occur in groups of two or more, often spread over hundreds of hectares (Stock 1991). Attack rates of western balsam bark beetle in southern B.C. can range from 0.7 to 1.6% of subalpine fir annually in a stand, depending upon ecosystem (Maclauchlan 2016). The beetle attacks large-diameter, standing live trees and downed subalpine fir. Western balsam bark beetle consistently attacks trees from the largest-diameter classes in each stand, but the mean diameter of attacked trees between sites may vary significantly (ranging from 10 cm diameter at breast height to over 50 cm), indicating that factors other than diameter contribute to the susceptibility of subalpine fir to western balsam bark beetle (Bleiker *et al.* 2003). Susceptibility has been associated with tree diameter, age, recent radial growth, and induced resinosis (Bleiker *et al.* 2003). Although cumulative mortality can reach significant levels in chronically infested stands (Garbutt and Stewart 1991; Maclauchlan 2016), western balsam bark beetle may be less aggressive or exhibit unique attack dynamics compared to other tree-killing bark beetles at epidemic levels. Beetle populations persist within a stand for many years until most of the mature subalpine firs are killed (Garbutt 1992; McMillin *et al.* 2003). This selective and patchy distribution of mortality suggests that western balsam bark beetle may be limited by the abundance and distribution of susceptible hosts, as well as the harsh environment in which they live.

Many researchers (Hansen 1996; Gibson *et al.* 1997; Negrón and Popp 2009; Stock *et al.* 2013) have concentrated primarily on the flight periodicity and insect activity within subalpine fir stands. A paucity of work has been done on life-stage development of the western balsam bark beetle primarily due to the remote nature of most subalpine fir forests. In B.C., adults generally emerge in late June and fly until late July, locating suitable host trees through kairomones and primary attraction, at which point the males initiate construction of nuptial chambers beneath the bark (Bright 1976; Garbutt 1992; Stock *et al.* 2013). The species is polygamous, with males often attracting three or more females in a nuptial chamber. Females mate, then lay eggs in brood galleries that radiate out from the nuptial chamber, and toward the end of August will construct feeding and hibernation niches (Bright 1976) for the winter. Mature females may resume laying eggs the following year within hosts that have adequate phloem resource, whereas females within trees that are fully occupied with brood may emerge mid-summer to locate new hosts (Bright 1976). In addition to the main attack flight, comprised of males and females, an additional smaller flight, largely comprised of parent females (Hansen 1996; Gibson *et al.* 1997; Stock *et al.* 2013), has been observed later in the summer. In this late-season second flight, the females join existing gallery systems and often create hibernation niches.

Mathers (1931) first described the life cycle of the western balsam bark beetle in B.C., demonstrating that it completed its life cycle within two years. Bright (1963) subsequently speculated that the insect might be capable of completing its life cycle in only one year in the western and southwestern United States. Whether the brood is capable of developing to the adult stage in one year has not been shown. Insects have different strategies to cope with fluctuating weather conditions and phases of growth and dormancy: some undergo hormonally controlled diapause (obligatory diapause) that prevents insect development even when environmental conditions are good (Gilbert 1990), while others only undergo diapause when induced environmentally (facultative diapause). The spruce beetle, *Dendroctonus rufipennis* Kirby, is known to have a life cycle that can vary in duration, from one year up to three years, depending on climatic conditions and suitability of host material available (Knight 1961; Schmid and Frye 1977; Hansen *et al.* 2001; Bentz *et al.* 2010). Johansson *et al.* (1994) describe a flexible generation time for *Dryocoetes autographus* (Ratz.), a circumpolar species, that has expanded its range in Norway north, with the establishment of its host species, spruce. Swift and Ran (2013) noted that climate change may have a pronounced effect on high-elevation forests and associated insects. Therefore, a greater understanding of the developmental requirements for western balsam bark beetle is needed.

This study focuses on western balsam bark beetle life-stage development in standing and down subalpine firs, and flight periodicity over a range of elevations in southern B.C. We also studied the relationship of temperature to western balsam bark beetle development in standing and down host material. These trials were conducted in 1998, 1999, and 2002 at various field sites in southern B.C.

## MATERIALS AND METHODS

The developmental biology of western balsam bark beetle was investigated in the field by flight periodicity trapping, sampling of *in situ* life stages, and weather monitoring. These studies focused on the two very different stages in the beetles' life history: 1) emergence and flight dispersal and, 2) brood production and maturation within the host tree. On-site weather monitoring was used to determine critical threshold subcortical (phloem) temperatures for flight and development.

Seven field sites were selected throughout the southern interior of B.C. in subalpine fir ecosystems with active populations of western balsam bark beetle. Two sites, Cherry Ridge and Sun Peaks, were used in all three studies, while the other sites were used for monitoring flight dispersal timing only (Table 1).

One micro-logger–based climate station (Campbell Scientific Inc.) was set up at each of the Sun Peaks and Cherry Ridge sites to monitor ambient, duff and phloem temperature of western balsam bark beetle-attacked trees. The Sun Peaks and Cherry Ridge climate stations were located on the north aspects of standing trees within close proximity (±10 m) of other attacked trees, where flight dispersal monitoring and detailed life-stage studies were conducted. The Sun Peaks climate station was set up on June 18, 1998, and again on June 15, 1999. The climate station was installed next to a standing tree, and thermocouples were inserted three meters up the bole in the phloem of five nearby attacked subalpine fir. Thermocouples were inserted into western balsam bark beetle entrance holes. Thermocouples were also placed in the phloem on downed trees. Ambient air temperature was recorded at the relative humidity sensor on the climate station. Another climate station was installed on June 16, 1999, at Cherry Ridge, as per Sun Peaks. Numerous variables were recorded, but only date and phloem temperature were used for analyses in this study. On August 5, 1999, the climate station at Cherry Ridge malfunctioned, and no further weather data were recorded.

In 1998, three 8-funnel (8 plastic funnels aligned vertically over each other) Lindgren multiple-funnel traps (Lindgren 1983) were erected between June 18 and August 31 at Sun Peaks and monitored regularly for western balsam bark beetle flight activity. Traps were placed along an elevation gradient (1,450 m; 1,650 m; 1,850 m), and all traps were positioned just inside the stand edge. Each trap was hung on an aluminum pole, with the top of the trap approximately two meters above the ground. Traps were baited with the commercially available (±)-*exo*-brevicomin (release rate 0.4mg/24 h) bait for western balsam bark beetle (supplied by Phero Tech Inc., Delta, B.C., Canada, and now available through Distributions Solida Inc., Scotts Miracle-Gro Company).

In 1999, trapping trials were established at Sun Peaks and Cherry Ridge sites to follow the flight timing and activity of western balsam bark beetle. Four traps were hung at Sun Peaks over an elevational range at 100–150 m intervals (1,450 m–1,850 m), and two traps were hung at 1,650 m at Cherry Ridge. Weekly trap catches were collected from June 16 to October 9 at Sun Peaks. At Cherry Ridge, collections were made at irregular intervals from June 15 to October 30.

In 2002, a more comprehensive trapping trial was conducted, using nine sites (three traps per site) in six geographic locations (Table 1) within four ESSF subzones. Lindgren funnel traps were set up in a triangular formation, with the traps being approximately 20 metres apart. Traps were established from May 29 to June 21, with regular collections beginning June 19 until September 27. During the peak flight period, trap collections were made more frequently, up to three times per week, until the peak flight was over.

**Table 1**
Western balsam bark beetle study locations (1998, 1999, and 2002) with Engelmann Spruce–Subalpine Fir (ESSF) subzones listed for each site.

| | | UTM | | | | Study (year conducted) | | |
|---|---|---|---|---|---|---|---|---|
| Locations | BEC[a] | Zone | northing | easting | Elev. (m) | Dissections | Trapping | Weather |
| | | | | | | | 1998–1999 | |
| Sun Peaks | ESSFdc | 11 | 5642523 | 296600 | 1,450–1,850 | 1999 | 2002 | 1998–1999 |
| Cherry Ridge | ESSFwc | 11 | 5573800 | 394250 | 1,650 | 1999 | 1999 | 1999 |
| Spius Creek | ESSFmw | 10 | 5539281 | 633130 | 1,470–1,635 | | 2002 | |
| Torrent Creek | ESSFwc | 11 | 5603075 | 387147 | 1,685 | | 2002 | |
| Apex Mountain | ESSFxc | 11 | 5478306 | 289090 | 1,670–1,900 | | 2002 | |
| Buck Mountain | ESSFxc | 11 | 5549029 | 360134 | 1,750 | | 2002 | |
| Sunset Main | ESSFxc | 11 | 5527100 | 700200 | 1,820 | | 2002 | |

[a] ESSF subzone descriptions: dc=dry, cold; wc=wet, cold; mw=moist, warm; and xc=very dry, cold.

All insects collected from the trapping trials were stored in zip-lock bags, labeled, and frozen until processed in the laboratory, where each sample collection was then counted and the western balsam bark beetles were sexed.

Trap catch results were compared to daily weather patterns at sites with climate stations. The maximum and minimum phloem temperatures were plotted against trap catch to interpret the relationship between insect flight and subcortical temperature.

The literature describes western balsam bark beetle as having a two-year life cycle (Mathers 1931; Bright 1976). To capture all life stages (from initial attack through newly emerged adults), sample trees meeting specific criteria were selected in 1999 at the Sun Peaks and Cherry Ridge study sites. External signs and symptoms, such as foliage fade, and presence of entrance holes and frass on the bole, were used to select candidate trees and ascertain year of attack. Western balsam bark beetle tree baits ((±)-*exo*-brevicomin; release rate 0.4mg/24 h) were attached to two standing live and two freshly felled subalpine firs in early June 1999 to induce western balsam bark beetle attack. Downed trees were felled into the stand, where they were well shaded, and no limbs were removed. Both standing and down (natural blowdown) subalpine fir attacked by western balsam bark beetle in 1997 or 1998 were selected for sampling in 1999 to determine if there were obvious developmental differences between these two host scenarios. Six trees at Sun Peaks and three trees at Cherry Ridge were suitable for sampling (Table 2). All sample trees were in close proximity (±10 m) to the climate stations. Sampling took place at weekly intervals between June 15 and September 20, 1999. A rigorous sampling procedure was followed at each sampling date to help interpret progression of attack and tree symptoms. For each sample tree, numerous foliar attributes and bole symptoms were recorded, but only the ones used in the analysis are described. In some cases, particularly in the trees that were attacked in 1997, a comment was made at each dissection as to the abundance of exit holes. A ladder was used to access western balsam bark beetle attack found higher on the bole, up to 3.5 meters. A 20-cm x 20-cm template was centered over an entrance hole, and the bark was carefully removed to expose the gallery system. Gallery systems (Figure 1) were described to help elucidate the stage in the life cycle and productivity. All western balsam bark beetle life stages present (eggs, larvae, pupae, and parent and teneral adults) were collected and placed in vials of 70% ethanol for future processing in the laboratory.

Head capsule measurement is a commonly used method to determine the instar of immature insects (Bleiker and Régnière 2014). The head capsules of all western balsam bark beetle larvae collected in the field were measured using a dissecting microscope. Every measurement was taken at 4.5 X magnification, which yielded a micrometre measurement of 0.022 mm. Measurements were taken across the widest portion of the sclerotized head capsule. All head capsule measurements were sorted in ascending order and plotted to display frequency distribution. The lowest frequency class between peaks on a histogram can be used as the cut-points for each instar and are often visually determined (Logan *et al.* 1998; Bleiker and Régnière 2014). From these frequency distributions, delineation of instars was determined by visually identifying cut-points. Each instar was assigned a head capsule size range. All larvae collected were then given an instar designation and these data were then compared to field temperatures and date of field sampling. These comparisons provided the interpretations of life-stage occurrence and duration in standing and down trees.

## RESULTS

Very few beetles were caught in 1998 at the Sun Peaks site (170 beetles over 75 days), with the highest trap catches occurring July 6 and July 10. In 1999, at the Sun Peaks site, peak trap catch occurred between July 27 and August 8, with 64 beetles collected July 27 and 40 beetles collected August 8. There were additional small trap catches until early September (158 beetles in total). In 1999, at the Cherry Ridge site, 605 western balsam bark beetles were caught in two funnel traps, with the maximum number of beetles collected on August 3, similar in timing to insects collected at the Sun Peaks.

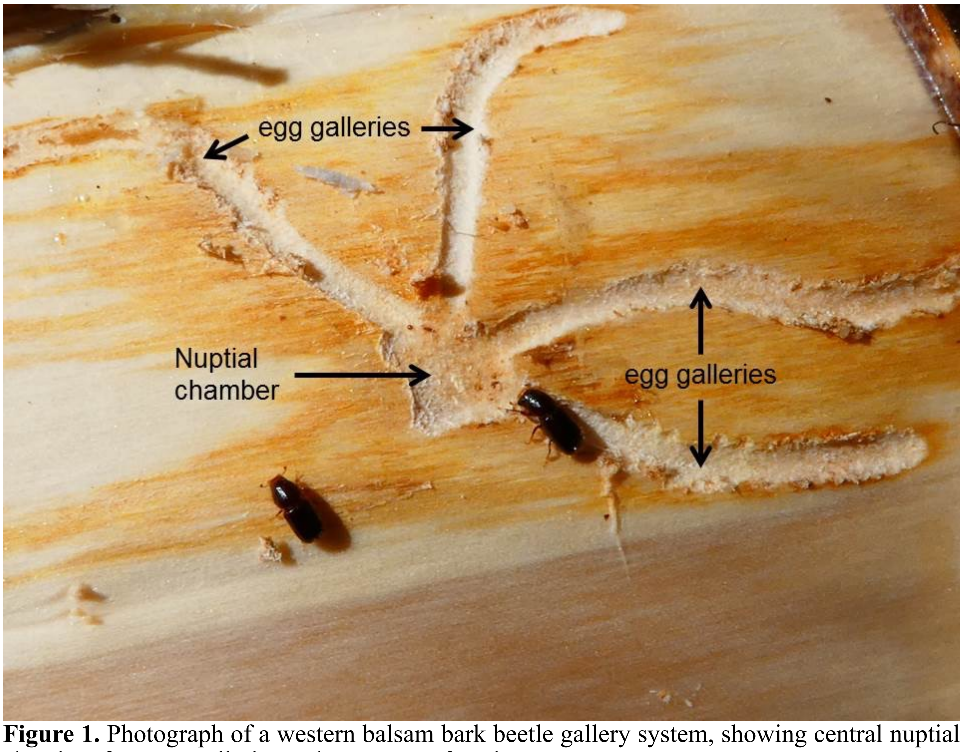


**Figure 1.** Photograph of a western balsam bark beetle gallery system, showing central nuptial chamber, four egg galleries and two parent females.

In 2002, insects were collected regularly from six additional sites, then counted and sexed (Figure 2). In total, in 2002, 348 trap samples at nine sites were collected and assessed, with 4,897 western balsam bark beetles caught from June 24 to September 10. Significantly (t test, $p<0.05$) more males than females were trapped early in the flight season (Figure 2). After July 9, 2002, equal or fewer male than female beetles were trapped.

Western balsam bark beetles were collected from traps beginning in mid- to late June, with the exception of one high-elevation site at Spius Creek, west of Merritt, B.C., where no beetles were collected until mid-July (Figure 3). At Sun Peaks, where there were three trapping sites on an elevational gradient, beetle flight occurred earlier at the lower-elevation site, gradually increasing in insect numbers later in the season at the higher-elevation site. Smaller numbers of beetles were caught at the high-elevation site at the onset of the flight period, with the majority trapped from July 9–20 (Figure 3). Although sites at or above 1,600 meters in elevation had high trap catches (Figure 3), there was no significant difference ($p \geq 0.05$) in mean trap catch numbers at the different elevations (1,450 m–1,600 m; 1,600 m–1,750 m; 1,750–1,900 m). There was no significant difference in trap catch numbers between the ESSF subzones, where the traps were located.

A second lesser flight beginning in late August was evident at Spius Creek, Torrent Creek, Sun Peaks, and Apex in 2002. At Sun Peaks, beetles were caught in varying numbers throughout the main flight period and into the second. Beetles were trapped in high numbers at all three Sun Peaks sites, with the highest catch at the mid-elevation site

(1,535 m) from June 24 to July 9. An elevational cline was observed at Sun Peaks, with most beetles caught in the upper-elevation site (1,850 m) (July 9 through July 19), when trap catches at the mid- and low-elevations sites were declining (Figure 3). This second flight was small and comprised approximately 7% of the total number of insects trapped at all study sites.

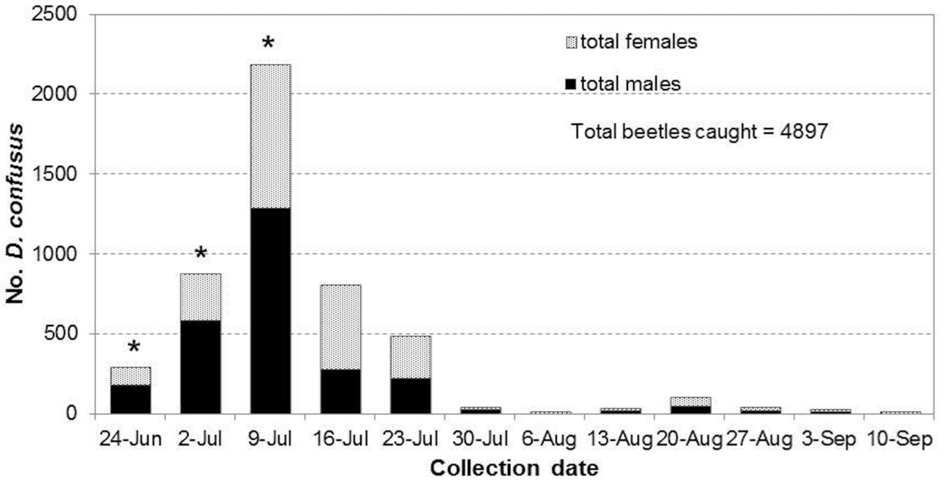


**Figure 2.** Total number of western balsam bark beetles collected during the 2002 flight period from 348 traps at nine sites in the southern interior of B.C., from June 24 to September 10. Asterisk above bars indicates significantly (t test, $p<0.05$) more males than females were trapped. Total number beetles caught = 4897.

Not one of the four baited subalpine fir trees was successfully attacked in 1999. Numerous beetles had initiated attack on the baited trees, as evidenced by the presence of entrance holes and frass. However, minimal egg galleries and brood were found in samples. From the nine non-baited trees attacked in 1997 and 1998, 7,257 life stages were dissected and preserved for further study in the laboratory (Table 2).

Head capsule sizes ranged from 0.276 mm to 1.058 mm wide. Three distinct peaks emerged from the measurements. First instar larvae ranged from 0.276 mm to 0.437 mm (0.379 ± 0.005 mm, mean ± S.E.); second instar larvae from 0.460 mm to 0.644 mm (0.549 ± 0.002 mm); and third instar larvae from 0.667 mm to 1.035 mm (0.826 ± 0.001 mm), with only two larvae with head capsules measuring 1.058 mm. Our data clearly show three distinct larval instars based on head capsule size frequency distribution, and there are not enough individuals from this study to confirm the possibility of a fourth instar. Figure 4 illustrates the distribution of head capsule widths for larvae collected from the attacked sample trees at Cherry Ridge and Sun Peaks sites. In total, 5,052 western balsam bark beetle larval head capsule widths were measured.

A summary of life stages found in 1999 from subalpine fir attacked in 1997 and 1998, at Sun Peaks and Cherry Ridge, are presented as proportional data in Table 2. Although life stages were dissected out of and counted from the 1997-attacked trees at Sun Peaks, new adults had emerged prior to the onset of sampling. Therefore, emergence holes were noted, but exact counts were not possible at that time.

In 1999, at Cherry Ridge, 3,442 life stages were dissected from three trees attacked in 1998. Two trees were standing attack, while the third tree was down on the ground. Although the two standing trees contained variable numbers of beetles, the proportion of each life stage dissected from the trees was similar (Table 2). This was in contrast to the life stages dissected from the downed attacked subalpine fir, where, by the end of the summer, only 4.5% of the insects dissected from this tree were teneral adults, compared to 18.3% and 21.7% of those dissected from the standing attacked trees. A similar pattern existed in the 1998-attacked trees from Sun Peaks, where development was slower and a smaller proportion of insects reached the teneral adult stage in the attacked downed trees (Table 2, Figure 5).

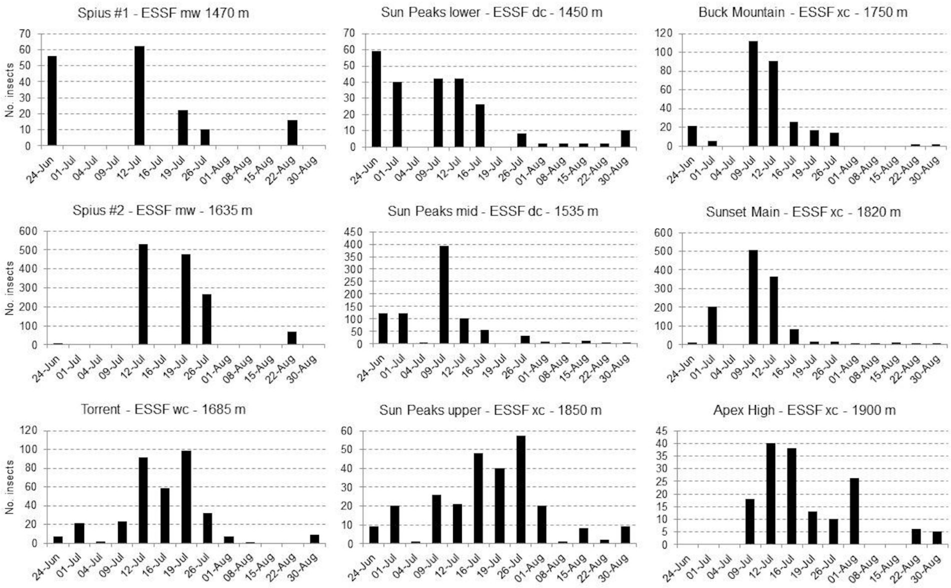


**Figure 3.** Comparison of western balsam bark beetle trap catches at nine sites in the southern interior of B.C. (2002) from June 24 to August 30. Number of beetles caught (N) is shown for each location.

There was a demarcated transition between life stages in all three standing trees shown in Figure 5. Late-instar larvae were present June through mid-July, followed by a 3–4 week transition to pupae. At the end of August and into September, the majority of life stages identified were teneral adults. In contrast, brood in down trees shown in Figure 5 displayed much slower development. Late-instar larvae were the predominant life stage found throughout August in downed trees. The transition from larvae to teneral adults was much slower in downed trees than in standing trees (Figure 5).

Seasonal temperature data collected from the phloem of trees by climate stations at Sun Peaks and Cherry Ridge in 1998–1999 were summarized into hourly and daily minimums, maximums and averages. The Sun Peaks climate station malfunctioned in 1999, therefore temperature data were not collected until July 25. Figure 6 shows minimum and maximum daily phloem temperatures at Cherry Ridge from May 20 to August 31, 1999. The recorded temperatures were similar until early July, when the minimum temperatures collected from the phloem of standing trees became significantly higher (t-test $p<0.05$) than the phloem temperatures recorded on the downed tree. No beetles were caught in baited traps until the minimum daily temperature in the phloem reached approximately 5° C. The same trend was observed from temperature data collected from Sun Peaks. The difference in minimum daily phloem temperatures between standing and downed trees was greater than the difference in maximum daily phloem temperatures on standing and downed trees. Only in mid- to late August did maximum daily phloem temperatures diverge significantly between standing and downed trees (Figure 6).

**Table 2**
Description of subalpine firs sampled at Sun Peaks and Cherry Ridge in 1999 and summary of proportional life stages present. Year of attack was noted for each sample tree.

| | | | | | Proportion of insects by life stage | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | Tree | Total no. | Instar | | | | Teneral |
| Location | Elevation (m) | Attack year | description | insects | 1 | 2 | 3 | Pupae | adults [a] |
| Sun Peaks [b] | 1,450 | 1997 | Standing-1 [a] | 46 | 0 | 6.5 | 69.6 | 0 | 23.9 |
| | 1,535 | | Down-1 [a] | 206 | 0 | 0 | 35.9 | 3.4 | 60.7 |
| | 1,535 | 1998 | Standing-2 | 957 | 2.8 | 1.9 | 48.2 | 12.9 | 34.3 |
| | 1,535 | 1997–1998 | Standing-3 | 496 | 0 | 3.6 | 55.2 | 21.4 | 19.8 |
| | 1,535 | 1997–1998 | Down-2 | 310 | 0 | 1.9 | 62.9 | 26.5 | 8.7 |
| | 1,850 | | Down-3 | 1,800 | 0.7 | 18.7 | 57.8 | 22.1 | 0.7 |
| Cherry Ridge [c] | 1,650 | 1998 | Standing-4 | 1,437 | 0 | 0.5 | 56.9 | 24.4 | 18.3 |
| | 1,650 | | Standing-5 | 502 | 0.2 | 0.4 | 52.6 | 25.1 | 21.7 |
| | 1,650 | | Down-4 | 1,503 | 0 | 0.5 | 82.2 | 12.8 | 4.5 |

[a] Some new adults (tenerals) had emerged prior to the onset of sampling as evidenced by the presence of exit holes. Relative abundance of exit holes was noted, but not counted at the time of dissection.
[b] Sun Peaks sampling dates: June 15, 22, 28, July 6, 13, 20, 29, August 3, 10 16, 26, and September 3, 7, 13, 20, 1999.
[c] Cherry Ridge sampling dates: June 16, 24, July 2, 9, 15, 22, 27, August 5, 11, 20, 23, and September 2, 7, 13, 20, 1999.

Some early flight of western balsam bark beetle at Cherry Ridge may have been missed due to traps not being in place until June 15, 1999. Sustained catches of western balsam bark beetle occurred from early July through September. The combination of exceeding a 5° C subcortical (phloem) daily minimum temperature and reaching or exceeding 20° C subcortical maximum temperature appeared to initiate beetle emergence and flight. There may have been minimal flight prior to trap placement when both these parameters were met (Figure 6; June 10–June 17). Trap data from sites of similar elevation did not have significant trap catches prior to July.

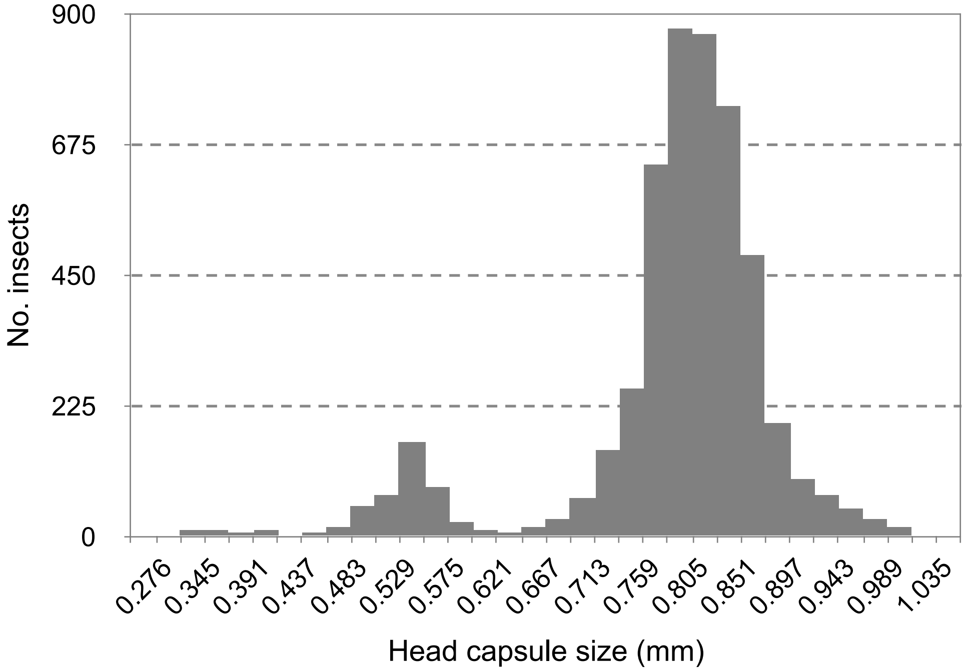


**Figure 4.** Frequency distribution histogram and estimation of larval instar for western balsam bark beetle. A total of 5,052 head capsules were measured.

## DISCUSSION

Our study confirmed the primary flight of western balsam bark beetle occurred from late June through July, depending on site and elevation (Hansen 1996; Gibson *et al.* 1997; McMillin *et al.* 2001; Negrón and Popp 2009; Stock *et al.* 2013). A much smaller, secondary flight occurred later in the season, comprised primarily of females re-emerging from the original host, either to initiate new brood galleries or to create hibernation niches (Maclauchlan, personal observations). Mathers (1931) reported a secondary flight occurring in mid- to late July; however, at the elevations monitored in this study, we only saw this flight beginning in mid-August. Others have also reported a later start to the secondary flight (Hansen 1996; Gibson *et al.* 1997; McMillin *et al.* 2001; Negrón and Popp 2009; Stock *et al.* 2013). Bark beetle flight and development are highly responsive to temperature (Hansen *et al.* 2001; Gaylord *et al.* 2008) and latitude (Williams *et al.* 2008; Bleiker and van Hezewijk 2016). Mathers' (1931) sites were at more northerly latitudes than our study areas, which could explain the difference in flight periodicity. Our results show that the western balsam bark beetle is flexible and may initiate flight earlier if weather conditions support beetle activity. This was seen at the Sun Peaks site, where beetle flight was initiated two weeks earlier in 1998 than in 1999. The former year was a record year for high temperatures in southern B.C. and across Canada

(Environment and Climate Change Canada, Government of Canada. Canada's Top Ten Weather Stories of 1998 (https://ec.gc.ca/meteo-weather/default.asp?lang=En&n=3DED7A35-1 Accessed on April 7, 2017).

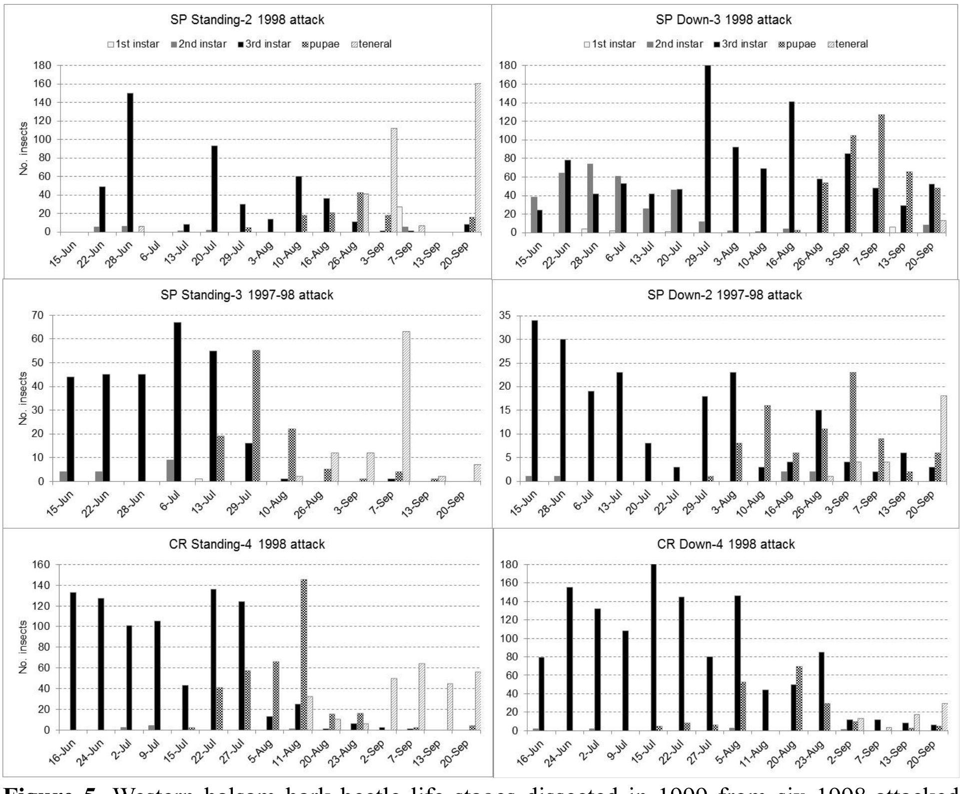


**Figure 5.** Western balsam bark beetle life stages dissected in 1999 from six 1998-attacked subalpine fir at Sun Peaks (SP) and Cherry Ridge (CR). Each sample measured 20 cm x 20 cm and was centered over an entrance hole.

Beetles generally initiated flight once minimum daily phloem temperatures reached or exceeded 5° C and maximum daily phloem temperatures approached 20° C or greater. Maximum daily ambient temperature as a threshold for flight in bark beetles has been determined in several studies (Stock 1991; Hansen 1996; Gaylord *et al.* 2008), and our determination of given site parameters is well within previously published data. Our observations and data clearly indicate that both minimum and maximum phloem temperatures are critical components to western balsam bark beetle flight activity and play an integral role in initiating emergence, flight and dispersal, as well as being an important factor in physiological development.

Subcortical, or phloem, temperature is likely an important factor for insect development. Western balsam bark beetle is active under the bark very early in the season, as evidenced by sawdust and frass being pushed out of entrance holes and movement of life stages under the bark when excised (Maclauchlan, personal observations). This activity has been observed as early as April, with flight not occurring for another two or more months (Maclauchlan, personal observations). This early activity highlights the fact that the physiological development of western balsam bark beetle proceeds within very different temperature limits than is required for flight initiation. Early season subcortical activity may allow female beetles from the late-season flight to initiate brood production very early the following summer, allowing brood increased developmental time. With the early onset of warm weather in spring and often long, extended summers, this potentially gives western balsam bark beetle better developmental conditions and ultimately could provide an opportunity to shorten their life history to one year, as suggested by Bright (1963).

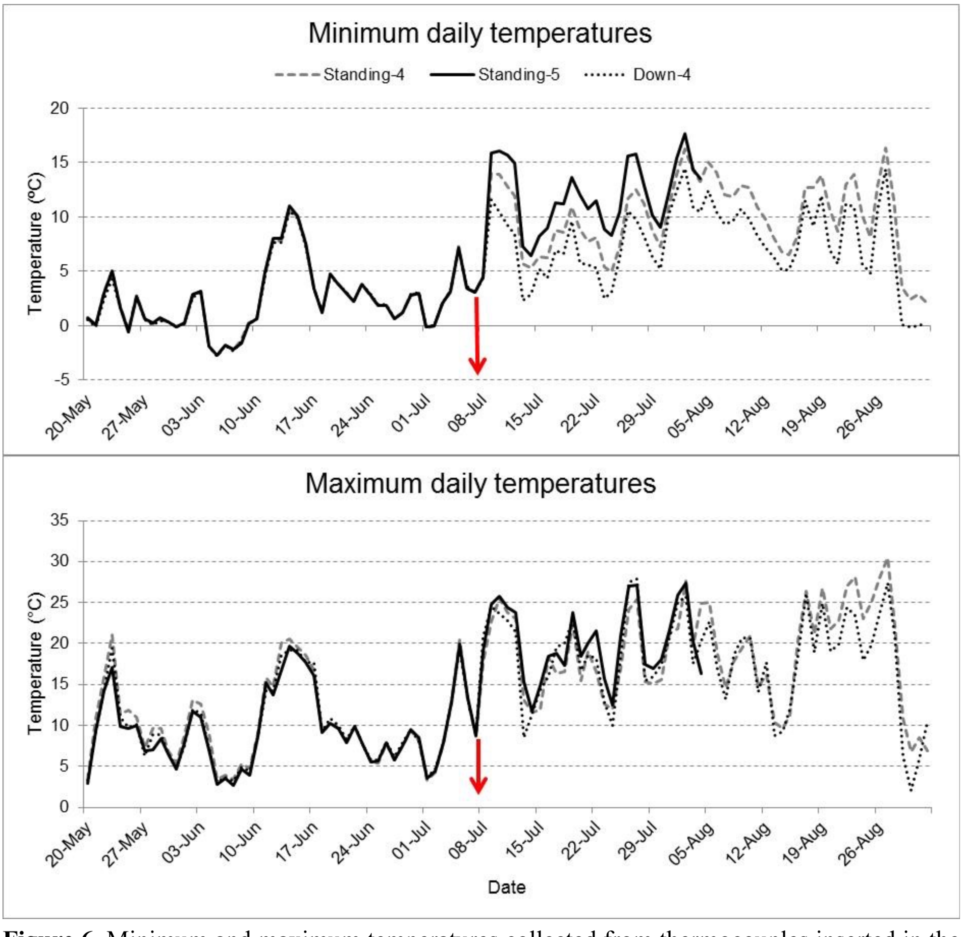


**Figure 6.** Minimum and maximum temperatures collected from thermocouples inserted in the phloem on three sample trees at Cherry Ridge research site, between May 20 and August 31, 1999. Arrow indicates date of first trap catch (July 8). Traps were established June 15 and checked weekly.

The field collections confirmed three distinct larval instars based upon their respective head capsule size range. The head capsule size range and average we found for first and second instar larvae fall within the range found by Stock (1981). However, our data do not clearly indicate a fourth instar; whereas Stock (1981) detected two overlapping head capsule populations, that he identified as third and fourth instars. Several larvae from controlled temperatures rearing conducted by the authors (unpublished data) had very large head capsules (greater than 1.035 mm), hinting at the possibility of a fourth instar; however, it was an uncommon occurrence in the field. The occurrence of fourth-instar larvae was much more prevalent in a controlled temperature setting (unpublished data) than in our field collections of life stages. Stock's (1981) data were also obtained from controlled temperatures rearing. Our field data suggest that diurnal fluctuations of subcortical temperature influence physiological development and may prevent a final molt to fourth instar. Late-instar larvae often have higher temperature thresholds for development than early instars do, preventing progression to cold-susceptible advanced life stages before the onset of winter (Safranyik and Wilson 2006). Under field conditions, the western balsam bark beetle may not have an obligate fourth instar.

Our results clearly elucidate that western balsam bark beetle developed more slowly in attacked down trees than in attacked standing trees. We hypothesize that this is due to host finding, host suitability, and a number of climatic factors. Host suitability and attack success may depend on timing of the tree falling (seasoning) (Dyer 1967), placement of the tree on the ground (touching the ground or somewhat elevated), and amount of shade or direct sunlight on the bole (Schmid and Frye 1977) that could affect heat sums needed for beetle development. Blowdown events are relatively uncommon in subalpine fir stands, unlike the regular and often large-scale blowdown events seen in mature spruce stands (Woods *et al.* 2010). Thus, encountering downed trees is a relatively rare event for this bark beetle, and its search patterns for down material may not be as discerning as for vertical hosts. The highest frequency of blowdown is seen at stand edges (e.g., clearcut edges) and in natural openings (personal observations). Stand edges or more open stand scenarios might afford better ambient conditions for beetle development. Although downed trees may offer the beetles more moderated conditions in late fall through early spring due to the protective insulating characteristics of snow cover, this same snow cover is often retained longer into the spring, depending upon log placement in a stand, thereby keeping logs cool and delaying the onset of beetle development. Also, cooler temperatures in downed trees occur earlier in late summer than in standing trees (Figure 6). Although a good resource from the point of view that the beetles encounter little or no host resistance, it appears that beetle development is prolonged, potentially increasing vulnerability to parasites, predators, woodborer activity, and host deterioration.

Proportionally, four to five times the number of brood in standing trees attained the teneral adult stage prior to winter, compared to down trees at both sites. By the end of summer, less than 10% of insects dissected from 1998-attacked downed trees had reached the teneral adult stage. There was no indication that attack density differed between standing and downed trees (Table 2) (Maclauchlan 2003), and large numbers of larvae developed in the downed trees. However, the cooler and shorter season available to beetles in downed trees suggest they are less suitable hosts for western balsam bark beetle.

Both standing and downed subalpine firs were baited in 1999 to induce attack. Although beetles initially responded to the bait and began excavating nuptial chambers, the weekly sampling demonstrated that none of the trees was successfully mass attacked. This has been observed in the past, where trees baited for western balsam bark beetle, both standing and down, have high levels of unsuccessful attack, compared to natural attacks occurring in close proximity (Maclauchlan *et al.* 2003; personal observation). Bleiker *et al.* (2003) determined that western balsam bark beetle had discerning host-selection capabilities, and parameters associated with host quality that the beetles are able to detect may assist in subsequent developmental success.

Our results clearly revealed a two-year life cycle for western balsam bark beetle in southern B.C. Additional work is needed to determine if western balsam bark beetle larvae or teneral adults require a cold period, or if they can undergo continuous development, as seen in the spruce beetle (Schmidt and Frye 1977), if growing seasons lengthen. The presence of fourth-instar larvae in laboratory rearing suggests that a cold period may be needed or conversely that western balsam bark beetle has evolved a mechanism to postpone the pupation or eclosion process until warmer temperatures trigger it (Johansson *et al.* 1994). Information on the response of this insect to changing habitat conditions as our high-elevation forest habitats continue to warm may be useful in future forest planning, harvest and management.

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