The balsam bark weevil, *Pissodes striatulus* (Coleoptera: Curculionidae): life history and occurrence in southern British Columbia

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ABSTRACT

Subalpine fir (*Abies lasiocarpa* (Pinaceae)) forests in British Columbia (B.C.) are increasingly climate-stressed and vulnerable to pest damage. Following a drought in southern B.C., the balsam bark weevil, *Pissodes striatulus* (Coleoptera: Curculionidae), was observed attacking and killing mature subalpine fir trees. This study documents *P. striatulus* as a tree-killing insect, often associated with western balsam bark beetle (Coleoptera: Curculionidae), which is considered the most destructive insect pest of subalpine fir. In B.C., this weevil displays a one-year life history, overwintering as late-instar larvae in the bark and as newly emerged or older adults in the duff at the base of attacked trees. Attacked trees are difficult to identify until the tree becomes chlorotic and dies. Larvae may excavate diagnostic chip cocoons in the sapwood before pupating, but most complete their development in the phloem where their galleries quickly become obscured by woodborer activity and other insects. *Pissodes striatulus* was found at 71% of sites surveyed, and 19% of trees sampled were killed by the weevil acting as the primary invader. The weevil uses downed trees, slash, and susceptible live trees, is long lived, and can switch from primary to secondary attacker, demonstrating its capacity to adapt to available and changing conditions.

Key words: balsam bark weevil, *Pissodes striatulus*, subalpine fir, climate stress

INTRODUCTION

Over the past two decades, subalpine fir *Abies lasiocarpa* (Hook.) Nutt. (Pinaceae) mortality in British Columbia (B.C.) has increased due to insect attack, root disease, and climatic stress (Maclauchlan 2016). Much of this mortality is attributed to the western balsam bark beetle (WBBB), *Dryocoetes confusus* Swaine (Coleoptera: Curculionidae), largely considered the most destructive insect pest of subalpine fir and causing scattered mortality over large areas of high-elevation forests (Furniss and Carolin 1977; Stock 1991; Garbutt 1992; McMillin *et al.* 2003; Lalande *et al.* 2020). Although the primary mortality agent may be WBBB, there is little ground survey information on the incidence and impact of WBBB and other damaging agents in these sensitive and often remote high-elevation forests.

Subalpine fir ecosystems are threatened by climate extremes, pests, and increased harvesting (Reich *et al.* 2016; Lalande *et al.* 2020). These are extremely valuable forests due to their inherent hydrologic contribution (Winkler *et al.* 2017), carbon sequestration, and habitat attributes. Subalpine fir grows well at high elevations, from 600 to 2250 metres, throughout most of the B.C. interior (Parish and Thomson 1994). In the mountains and plateaus of interior B.C., subalpine fir is often associated with spruce (Pinaceae) and is a major component of the interior high-elevation forests from Yukon, Canada, to Arizona, United States of America. Cool summers, cold winters, and a deep

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snowpack are important in determining where subalpine fir grows well (Parish and Thomson 1994).

As more non-native insects establish and expand in B.C. and climate change increases in intensity, many forest insects and fungal pathogens, both native and non-native, are expected to expand their ranges northwards and to higher elevations and, with this expansion, bring more severe impacts to newly invaded areas (Bentz et al. 2010; Woods et al. 2010, 2017; Haughian et al. 2012). The expansion of mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae), well beyond its historic range into northern B.C., Yukon, and Northwest Territories (Safranyik et al. 2010), coupled with the beetle’s extensive attack in young lodgepole pine (Maclauchlan et al. 2015), is a well-documented example of a native insect responding to the effects of climate change on both insect and host.

Another recent example of insect range expansion in B.C. is that of the balsam woolly adelgid, *Adelges piceae* (Ratzeburg) (Hemiptera: Adelgidae), an introduced insect from Europe. It was thought to be contained in a provincial quarantine zone on the B.C. coast until recent surveys (Zilahi-Balogh et al. 2016; Maclauchlan and Buxton 2018) confirmed its presence outside the pre-2014 quarantine zone, affecting subalpine fir throughout the southern interior and as far north as Horsefly in the B.C. Cariboo Region.

While conducting studies on WBBB in subalpine fir forests (Maclauchlan and Buxton 2016, 2017; Maclauchlan 2020), a weevil was observed attacking and killing live, mature subalpine fir trees, acting as a primary invader, much like tree-killing bark beetle species. The weevil was identified as the balsam bark weevil, *Pissodes striatulus* (Fabricius) (Coleoptera; Curculionidae) (Randall 1838; O’Brien and Thompson 1986). Most published records of this weevil are from eastern Canada, primarily Ontario, Quebec, and New Brunswick, and the northeastern United States of America, where reports have noted it infesting balsam fir, *Abies balsamea* (L.) Mill. (Pinaceae) that has been severely defoliated or killed by eastern spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae) (Swaine et al. 1924; Craighead 1950; Belyea 1952a). In B.C., there are very few published records for *P. striatulus*, and it has typically been observed in association with WBBB. Little is known of the life history, host selection parameters, and habits of this weevil in B.C.

Swaine et al. (1924) considered *P. striatulus* to be the most aggressive of the insects that attacked dead and dying trees following eastern spruce budworm defoliation. According to his studies, the larvae were reported never to develop to maturity unless the tree was almost dead, and two or three successive attacks could be made on the same tree before the tree’s resistance was low enough that weevil larvae could survive and mature to adulthood. Most observations from eastern forests describe *P. striatulus* as essentially a secondary insect (Craighead 1950). Secondary insects usually select hosts that have impaired defenses and avoid vigourous trees, whereas primary invaders attack and kill apparently vigourous trees through pheromone-mediated mass attacks. Early observations on the seasonal history of this weevil differ somewhat depending upon location (Swaine et al. 1924; Belyea 1952a, 1952b), suggesting it has a plastic life history and is able to adapt to local and seasonal climate. Belyea (1952a) observed full-grown larvae and pupae under the bark of infested trees in the Lake Nipigon area of Ontario, Canada, in late June, with adults emerging from late June through the middle of August, and the majority emerging in the last three weeks of July. They estimated development time to be just less than 12 months from egg to emergent adult in this area. Swaine et al. (1924), however, suggested a two-year life cycle, with the insects overwintering as adults and emerging from the duff in the spring to mate and lay their eggs. All studies found that the weevils preferred to oviposit on the lower fifth to lower half of their balsam fir host.

Other *Pissodes* species have similar host selection parameters to *P. striatulus*. *Pissodes nemorensis* Germar and *Pissodes schwarzi* Hopk., are attracted to boles, slash, and root collars of weakened, stressed, or dying trees (Finnegan 1958; United States Department of Agriculture Forest Service 1985; Atkinson et al. 1988; Maclauchlan et al.
Host selection by *P. nemorensis* and *P. schwarzi* has been shown to be pheromone mediated (Fontaine and Foltz 1982; Maclauchlan et al. 1993), with *P. nemorensis* producing grandisol (cis-2-isopropenyl-l-methylcyclobutanecethanol) and its corresponding aldehyde, grandisal, which act together as aggregation pheromones (Booth et al. 1983; Phillips et al. 1984; Phillips and Lanier 1986). *P. striatulus* may also use these pheromones and the smell of stressed trees to attract mates and aggregate on potential host trees.

The objectives of this study were to describe the occurrence, life history, and host preference of *P. striatulus* in susceptible stands of subalpine fir in southern British Columbia. Additionally, we aimed to determine the prevalence of *P. striatulus* attack in low-elevation, climate-stressed subalpine fir stands and its interaction with WBBB.

**METHODS**

**Life history sampling and field observations.** Three field sites were selected to study the life history of *P. striatulus* in southern B.C. A site located off the Spahats Creek Forest Service Road (51° 46' 25.18" N, 119° 45' 26.77" W; elevation: 1 600 m) northeast of Clearwater, B.C. in the Engelmann–Spruce–Subalpine Fir–Wet–Cold biogeoclimatic zone (ESSFwc) (Lloyd et al. 1990; Meidinger and Pojar 1991), and predominantly subalpine fir, was selected to collect observational data during the summers of 2015–2016. The other two sites, Watching Creek (50° 54' 23.64" N, 120° 26' 32.78" W; elevation: 1 375 m) and Antler Road (50° 52' 54.12" N, 120° 24' 39.96" W; elevation: 1 260 m) were located about 30 km northwest of Kamloops, B.C., on the west side of the North Thompson River. Both sites are situated in the Montane–Spruce–Dry–Mild biogeoclimatic subzone (MSdm). The Watching Creek site is composed of spruce, Douglas-fir, and subalpine fir. The Antler Road site is a mix of spruce and subalpine fir. From 2015 through 2017, both the Watching Creek and Antler Road sites had a high population of *P. striatulus*, and the sites were accessible throughout most of the year.

In 2016 through 2018, a total of 15 live, green subalpine fir trees that were newly mass attacked by *P. striatulus* at the Watching Creek and Antler Road sites were selected for twice-weekly life-stage sampling and observation (March–November). During field sampling, a ladder was used to access higher portions of the trees to collect bark samples, which were approximately 20 cm × 20 cm. Larvae and other life stages that were easily visible when the bark was removed were collected and placed into vials containing 70% ethanol (EtOH). Each remaining bark sample was placed in a sealable bag, labelled, and brought into the laboratory, where it was dissected to expose remaining life stages within one day of collection. All specimens were preserved in 70% EtOH for future measurement. Ten live adult weevils were collected and sent to L. Humble, Canadian Forest Service, Victoria, B.C., Canada, to confirm species identification. The following information was recorded at each field sampling: life stage(s) present; gallery description; timing of attack and oviposition; presence–absence of chip cocoons or exit holes; timing of adult emergence; and, bole and foliar symptoms of attacked trees. Adults collected during field sampling were frozen until measured. All life stage and field observations were compiled along a timeline to produce a life table for *P. striatulus* in southern B.C.

A Hobo™ U23-003 Pro v2 Temperature Data Logger, with 2 exterior sensors and a Hobo™ RSI Solar Radiation Shield (Onset Computer Corporation, Bourne, Massachusetts, United States of America; https://www.onsetcomp.com/) were set up at the Watching Creek and Antler Road sites to monitor daily minimum and maximum temperatures over a full year (January–December 2017). One temperature sensor was placed at ground level, and the second sensor was placed at 2.5 m on the north side of a tree situated inside the stand. Temperature records were downloaded to a laptop computer every two to three weeks. At the Watching Creek site, four 8-funnel Lindgren multiple-funnel traps (Lindgren 1983) were placed at 25-metre intervals throughout the stand. Two
traps were baited with (±)-exo-brevicomin to monitor WBBB flight times, and two were baited with grandisal and grandisol (supplied by Synergy Semiochemicals Corp., Delta, British Columbia, Canada), to monitor the onset of *P. striatulus* flight. The traps were checked when life-stage sampling was conducted at the sites. Average daily maximum and minimum temperatures were compared to trap catches and life stage sampling data.

In addition to the periodic sampling of trees, five additional live, green subalpine fir trees mass attacked by *P. striatulus* at the Watching Creek and Antler Road sites were felled to assess attack over the entire length of the trees, to collect life stages, and to quantify successful weevil emergence (Table 1). Each time an emergence hole was counted, an X was marked over the hole in indelible marker to ensure a single count. Felled trees were cut into one-metre sections, with the cardinal direction marked and labelled according to position in the bole, and then transported to the laboratory, where the final count of emergence holes was done. The cut ends of all sample sections were sealed with paraffin wax to prevent desiccation; each section was covered in mesh screening and placed in a 20 °C environment chamber to allow any further emergence. The diameter of each one-metre tree section was measured and the bark surface area calculated. The length and position of each section was converted to reflect height on individual trees. The diameter of a sub-sample of exit holes was measured. The data were converted to the number of emergence holes per square metre of bark surface, and the frequency distribution of emergence density by tree height was calculated.

**Table 1.** List of subalpine fir trees felled to assess emergence and extent of attack on trees, noting year of attack, date felled, site (Watching Creek: 50° 54' 23.64" N, 120° 26' 32.78" W; elevation: 1 375 m; Antler Road: 50° 52' 54.12" N, 120° 24' 39.96" W; elevation: 1 260 m), and dates each tree was field sampled.

<table>
<thead>
<tr>
<th>Attack year</th>
<th>Date felled</th>
<th>Site</th>
<th>Field sampling dates</th>
</tr>
</thead>
<tbody>
<tr>
<td>2016</td>
<td>16 Nov. 2016</td>
<td>Watching Creek</td>
<td>No field sampling</td>
</tr>
<tr>
<td>2017</td>
<td>18 Jun. 2018</td>
<td>Antler Road</td>
<td>5 Jul. – 22 Nov. 2017&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>a</sup> Observed undergoing mass attack by *P. striatulus* on 5 July 2017.

The head-capule widths of each collected larva were measured at the widest point using a Meiji binocular microscope (Meiji Techno, San Jose, California, United States of America) equipped with a micrometer to determine the number and size range of larval instars (Stark and Wood 1964; Langor and Williams 1998; Logan *et al.* 1998; Panzavolta 2007). The head-capule width data were analyzed using the Hcap program developed by Logan *et al.* (1998). Adult weevils collected during field or laboratory sampling were measured at their widest and longest points to determine size range.

Eleven longterm installations previously established to monitor WBBB attack and stand succession in subalpine fir forests in southern B.C. (Maclauchlan and Buxton 2017; Maclauchlan 2020) had occasional records of *P. striatulus* colonising trees within these plots. Plots were located in three ESSF subzones: three in the ESSFxc (very dry, cold); six in the ESSFwc (wet, cold); and two in the ESSFmw (moist, warm) (Lloyd *et al.* 1990; Meidinger and Pojar 1991). The weevil was observed colonising mature subalpine fir
alone and in association with WBBB. We summarised all records of *P. striatulus* from these 11 plots.

**Field surveys.** The objective of the field survey was to ascertain presence or absence of *P. striatulus* in randomly selected low- to mid-elevation subalpine fir stands by examining recently dead subalpine fir trees. Using Aerial Overview Survey spatial data (Ministry of Forests, Lands, Natural Resource Operations and Rural Development 2016), low- to mid-elevation stands containing subalpine fir and current WBBB attack (red trees) were identified. From the air, red subalpine fir is typically labelled as mortality caused by WBBB. Geo-referenced PDF maps were created for candidate areas, loaded onto a tablet, and using Avenza Systems Inc.® (2017; Toronto, Ontario, Canada) were located in the field. Survey sites were chosen based upon road access and visible red or fading subalpine fir near mapped areas of 2016 WBBB. Elevation and GPS coordinates were recorded for each site that was surveyed. Recently dead subalpine firs (displaying chlorotic to bright red foliage) were assessed for *P. striatulus* and other mortality factors. Occasionally, if older attack (displaying dull red foliage) or green trees undergoing current attack were present, they were also assessed. The number of trees assessed in each stand varied, based on the abundance of recently killed trees in the stand. Each tree was thoroughly checked by first examining the outer bark for exit holes and signs of oviposition or resin, and then peeling back the bark to look for weevil galleries, chip cocoons, and life stages. The foliage colour was recorded as green or chlorotic (new attack), bright red (prior year attack) and dull red (older attack). Western balsam bark beetle, woodborers, and any other insects or pathogens found under the bark were noted. All *P. striatulus* life stages were collected, labelled, and stored in 70% alcohol. For each sampled tree, existence of evidence of only *P. striatulus* attack, only WBBB attack, or whether both species were observed was recorded.

**RESULTS**

**Life history sampling and field observations.** The 10 weevil specimens sent to L. Humble were confirmed as *P. striatulus*, the balsam bark weevil (pers. comm.). The life table shown in Figure 1 was constructed by combining all field observations and life-stage sampling gathered in 2015 through 2017. On 2 July 2015, at the Spahats Creek site, numerous adult *P. striatulus* were observed mating and ovipositing on the freshly cut surface of a subalpine fir stump at the phloem–cambium interface and on the boles of standing live subalpine fir. Oviposition was distinguished by small feeding punctures made by the weevil in the outer bark, where it had laid one to several eggs and then had capped the puncture with a frass plug. At the oviposition site, a droplet of cloudy, red pitch (Fig. 2) usually was present, and the tree characteristically produced streams of resin. In late September, the bark was peeled from the attacked stumps, and the galleries originating from the cut surface were clearly visible radiating downwards to the root collar (Fig. 2). The larvae created straight or sometimes winding serpentine-like galleries downwards from the point of oviposition; as the larvae grew, they often veered off at right angles and mined around the circumference of the tree. By 25 September, larvae were large, late instar, and presumably in the overwintering stage. At that time, *P. striatulus* larvae (same life stage as in the stump) were also found in standing subalpine fir attacked by WBBB in 2014. Weevil attack occurred on the lower bole where there was available phloem not used by WBBB.

In October 2015, the Watching Creek site was first located by field-checking a fading subalpine fir that displayed a slightly different fade pattern than is normally associated with trees attacked and killed by WBBB, which typically fade to a bright red the summer following attack. This tree had dull red foliage with remnants of green on some branch tips (Fig. 2). Under the bark, galleries around the entire circumference of the tree, like those at the Spahats Creek site, and late-instar weevil larvae were found, indicating that attack had likely occurred that summer. The outer bark showed no sign of
attack by WBBB, nor was frass or sawdust present around the bole, as is usually the case with WBBB attack.

Figure 1. Timing of behaviour and life stages of *P. striatulus* from first to last observation (data from 2015–2017). Outliers are represented by ●.

Figure 2. From left to right: *P. striatulus* oviposition puncture with pitch droplet (July), larval galleries in phloem (October), foliage fade in October of subalpine fir trees attacked by *P. striatulus* earlier in the summer.

Observations and field sampling in 2016–2017 at the Watching Creek and Antler Road sites revealed that larvae were active under the bark by late April or early May from attack the previous summer. Larvae present near the phloem–sapwood interface were beginning to construct chip cocoons at that time. Sampling found that the majority of larvae within the bark layer did not score the sapwood. Slower development was noted on the north aspect of trees, near the ground, and in trees located well within the stand, where conditions were cooler and less sunlight could penetrate the canopy. Overwintering adults were found in the duff layer at the base of trees throughout May during the periodic field assessments. By mid-June, late-instar (large) larvae and pupae were most predominant under the bark, and adults were observed on tree boles, cut stumps, and in recent axe cuts on trees. From late June through mid-July, pupae and late-instar larvae (Fig. 3) were predominant, and through July, teneral and mature adults were found. Emergence peaked from late July into early September on trees that were attacked the previous summer, although some larvae and a few pupae could still be found.
Emergence holes were abundant on the southeast aspect (warmer side) of many trees (Fig. 3). By October, all trees attacked by *P. striatulus* earlier in the year contained large larvae (presumably third or fourth instar).

![Figure 3. Life stages and signs of *P. striatulus*: eggs (top left); larva in chip cocoon (top centre); pupa (top right); exit holes (bottom left); adult weevil in chip cocoon (bottom right) prior to emergence; and mating adults.](image)

Some trees attacked by *P. striatulus* in 2015 were subsequently attacked by WBBB in 2016. Trees were already fading, but some available phloem remained for WBBB to colonise. From late June through July, adult *P. striatulus* were observed mating and ovipositing on the boles of mature, live, outwardly healthy-looking subalpine firs at the Watching Creek and Antler Road sites. The first adult emergence at the Watching Creek site was observed on 11 July 2016. Therefore, weevils seen ovipositing could presumably both be overwintered and newly emerged adults. By 20 July, many small larval galleries were observed under the bark of newly attacked trees. On 5 July 2017, a large, live healthy subalpine fir at the Antler Road site was observed undergoing mass attack, with many adult weevils on the bole mating and ovipositing.

Temperature data were recorded throughout 2017 except for an 18-day period (25 May–12 June) when there was a malfunction, after which the temperature-recording device was replaced. Mating, oviposition, eggs, and early instar larvae were first observed when average daily minimum temperatures ranged from 5 °C to above 10 °C and average daily maximum temperatures ranged from 15 °C to above 25 °C. Pupae occurred when the average daily maximum temperature was from above 10 °C to the mid-20 degrees Celsius (Fig. 1; Fig. 4). Little or no development was noted after average daily minimum temperature was at or below 0 °C in late September to early October.

Based on trap catches at the Watching Creek site, two distinct flights by WBBB occurred. one in late June and the other in mid-August to mid-September. The later flight period was more prolonged. A few *P. striatulus* adults were caught in pheromone-baited traps on 5 July and 13 July 2017. Weevils were caught at the end of WBBB’s first flight period. Western balsam bark beetle were caught in traps once the average daily minimum temperature rose above 0 °C and the average daily maximum temperature surpassed 10 °C, while *P. striatulus* were caught in traps once the average daily minimum temperature surpassed 10 °C and the average daily maximum temperature was above 20 °C.
The three felled subalpine firs were just over 120 years old, and diameter at stump height ranged from 21.0 cm to 43.0 cm. Tree 2, the largest tree, was attacked from the base of the tree up to 21.0 m high and had the highest density of successful emergence, with a maximum of over 100 exit holes per metre of$^2$ bark area at 6.5 metres height (Fig. 5). The average number of exit holes along the bole between 4.0 to 15.0 metres was 70 exit holes per metre of$^2$ bark area. The smallest felled tree (Tree 1), at 21.0 cm diameter at stump height, had emergence from the stump end to 8.0 metres, ranging from 10 to 30 exit holes per metre of$^2$ bark area. In Tree 3 (31.0 cm stump diameter), most emergence occurred from 2.0 to 10.0 metres height, ranging from 4 to 28 exit holes per metre of$^2$ bark area (Fig. 5). Attack was found well into the crown area of all trees. The diameter of the top section from each tree ranged from 9.0 cm to 18.5 cm.

A total of 1 202 larval head-capsule widths were measured, with widths ranging from 0.4 mm to 2.2 mm (Table 2). The Hcap program (Logan et al. 1998) was used to determine instar classification (Fig. 6). Hcap did not produce a clear separation of instars; however, there appear to be four. The number of larvae within a range of head-capsule widths was plotted, and four probable instar delineations were identified (Fig. 6). Based on these delineations, the average head-capsule width ($\pm$ S.E.) and range were calculated (Table 2). No clear demarcation occurred between second and third or third and fourth instars, but the average size of fourth-instar head capsules was $1.6 \pm 0.15$ mm (Table 2).

The length and width of 54 adult weevils and the width of 66 exit holes were measured. The average length and width ($\pm$ S.E.) of $P.\ striatulus$ was $6.7 \pm 0.1$ mm and $2.6 \pm 0.05$ mm, respectively. Exit holes were very circular and easily recognised, with an average width ($\pm$ S.E.) of $3.3 \pm 0.1$ mm (Fig. 3).

$Pissodes\ striatulus$ was recorded in all 11 permanent sample plots previously established to monitor mortality caused by WBBB and other damaging agents. Stems per hectare of subalpine fir affected by the weevil ranged from 2 to 69, and tree mortality ranged from $<1\%$ to $6\%$. The weevil was found both alone in trees and in combination with WBBB. Incidence of the weevil varied by year and location, with two plots in the ESSFxc and one plot in the ESSFwc having the highest recorded incidence of $P.\ striatulus$ attack.

Field surveys. Fourteen geographic areas were surveyed for a total of 58 sites and 235 trees (Table 3) in the summer of 2017. Site elevation ranged from 1 257 m to 1 800 m.
One to eleven subalpine fir trees were assessed at each site, for an average of 4.1 ± 0.3 (± S.E.) trees per site. Western balsam bark beetle attack was recorded at 69% of the sites, and 60% of subalpine fir showed evidence of WBBB attack. *Pissodes striatulus* attack was confirmed at 71% of sites, and of all subalpine fir assessed, 29% had some level of weevil attack (Table 3). Nineteen per cent (45 trees) of the trees sampled were colonised only by *P. striatulus*, and in the absence of any other potential mortality agent (*e.g.*, root disease), it was apparent that the weevil killed these trees.

**Figure 5.** Number of *P. striatulus* exit holes (per square metre of bark) along the bole of three mass-attacked subalpine fir trees.

**DISCUSSION**

This study reveals that *P. striatulus* is a commonly found insect in subalpine ecosystems and that it regularly attacks and occasionally kills subalpine fir in lower-elevation, more climatically stressed stands in southern B.C. The weevil is likely ubiquitous throughout all subalpine fir ecosystems in B.C.; it is recorded in this study’s 11 permanent sample plots, which are distributed throughout southern B.C., and in northern B.C. (J. Robert, Ministry of Forests, Lands, Natural Resource Operations and Rural Development, Omineca Region, B.C. personal communication), as well as from Waterton north to near Grande Cache, Alberta (D. Langor, Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta, Canada, personal communication). *Pissodes striatulus* may act both as a primary attacker, killing live subalpine firs, and as a secondary attacker, usually associated with WBBB. Both insects are known to colonise trees exhibiting reduced vigour (Craighead 1950; Belyea 1952a; Bleiker *et al.* 2003) caused by age (senescence), climate stress such as drought, or pre-existing stressors such as defoliation or disease. This study’s observations show that *P. striatulus* and WBBB can both initiate attack on apparently healthy, live subalpine firs, with one or the other following in the secondary attacker role; both insects will attack freshly down trees or stumps (L. Maclauchlan personal observation.; Stock 1991; McMillin *et al.* 2003, 2017). The ability of the weevil to use downed trees and slash material and to switch roles between secondary invader colonising highly stressed or dead trees and primary invader attacking live, green trees demonstrates its capacity to adapt to changing and available conditions. The live, green subalpine firs observed being attacked by *P. striatulus* did not exhibit any outwards signs of stress or decline. Drought conditions may have predisposed
trees to attack by one or both insects; however, no obvious drought mortality was observed.

![Graph showing head-capsule width distribution and instar separation](image)

**Figure 6.** Head-capsule width distribution of *P. striatulus*. The line in the upper graph represents possible instar distribution (graph generated using Hcap; Logan et al. 1998). The lower graph shows frequency over a range of head-capsule widths and possible instar separation.

**Table 2.** Delineation of *P. striatulus* larval instars by head-capsule width.

<table>
<thead>
<tr>
<th>Instar</th>
<th>N</th>
<th>Average width (mm) (± S.E.)</th>
<th>Size range (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>30</td>
<td>0.5 ± 0.01</td>
<td>0.4-0.6</td>
</tr>
<tr>
<td>2</td>
<td>129</td>
<td>0.9 ± 0.01</td>
<td>0.6-1.0</td>
</tr>
<tr>
<td>3</td>
<td>520</td>
<td>1.3 ± 0.01</td>
<td>1.1-1.4</td>
</tr>
<tr>
<td>4</td>
<td>523</td>
<td>1.6 ± 0.01</td>
<td>1.5-2.2</td>
</tr>
</tbody>
</table>
Evidence that *P. striatulus* has killed or colonised trees may be difficult to detect. Unlike WBBB, which leaves diagnostic gallery traces etched into the sapwood, *P. striatulus* rarely does so. The weevil often spends its entire development period within the phloem–cork portion of the bark, where the traces of its galleries are quickly obscured by those made by woodborers and other insects (L. Maclauchlan, personal observation), that arrive after the weevil has initiated attack. Belyea (1952a, 1952b) reported that *P. striatulus* was sometimes associated with the woodborer, *Monochamus* spp. Dejean (Coleoptera: Cerambycidae) in balsam fir trees sampled in New Brunswick and Quebec, Canada, and Minnesota, United States of America, after the severe eastern spruce budworm outbreaks of the early 1900s. He suggested that *P. striatulus* could kill weakened balsam fir trees that had survived severe budworm defoliation, up to four years following the budworm outbreak. This supports the current study’s observations of *P. striatulus* contributing to the death of subalpine fir in ecosystems affected by disease or defoliation or in years following drought events. *Pissodes* spp. Germar may live up to four years (McMullen and Condrashoff 1973; Maclauchlan 1992; Langor and Williams 1998; Lewis et al. 2002), and this study records the presence of overwintered adults, suggesting that *P. striatulus* populations could potentially build up when stressed trees are abundant.

Trees attacked by *P. striatulus* alone have distinctive foliage-fade symptoms. Treetops fade rapidly during the summer and begin to shed foliage, while the lower branches of affected trees may turn red and lose foliage or they may retain some green foliage. Crowns are generally characterised by browning and dropping of needles. By the end of the summer, much of the foliage has dropped, and the attacked trees are a mix of red and grey. This differs from the foliar-fade symptoms observed after WBBB attack, which include the rapid, bright red colouration of foliage in the year following attack by WBBB. Mortality associated with WBBB is caused by a beetle–fungus complex, WBBB and *Ophiostoma dryocoetidis* (Kendrick and Molnar) de Hoog & Scheffer (Ophiostomataceae) (Molnar 1965; Garbutt 1992; Bleiker et al. 2005), and the fungus plays a vital role in the death of the host tree. There is no indication that *P. striatulus* has a fungal associate, which could in part account for the different symptoms displayed by the foliage of trees attacked only by the weevil.

Adult weevils are active from mid-June through to at least late August, showing a long biological window for finding suitable hosts, mating, and oviposition. Adults were found mating and ovipositing on trees before and throughout the emergence period of new weevils from attacked trees. Therefore, both overwintered (older) weevils and new adults could attack trees in mid-summer. The timing of attack can overlap with that of WBBB, highlighting the possibility that either insect can be the first coloniser. Lewis et al. (2002) demonstrated that *P. strobii* (Peck), a significant pest of young Sitka spruce, was capable of oviposition in the spring without needing to mate, if prior mating had occurred the previous autumn and the females were fecund. This may explain, in part, the long biological window. If long-lived adults are already fecund, synchronised emergence is less necessary to find mates and colonise novel habitats. It may also explain why pheromone-trap catches tend to be low in number for many species of *Pissodes* (Fontaine and Foltz 1982; Phillips and Lanier 1986; Nevill and Alexander 1992; Miller and Heppner 1999). Perhaps mating in this species occurs more frequently due to random encounters rather than sexual attraction through pheromone release.

*Pissodes striatulus* will mass attack a tree from ground level to the upper crown of trees. It prefers mature, large trees but, within a stand, can attack trees across a range of sizes. Successful weevil emergence was noted from upper tree sections as small as 9.0 cm in diameter. *Pissodes striatulus*, like many *Pissodes* spp., displays a very plastic life cycle, and development time can vary based on position of attack on the tree and annual weather conditions. Development near the root collar was slower than it was on the main bole and the warmer, east-facing aspects of attacked trees. Mating, oviposition, and larval development progressed rapidly during the warmest summer period, when average daily
minimum temperatures exceeded 0 °C and average daily maximum temperatures ranged from above 10 °C to 30 °C.

The length of the 54 *P. striatulus* adults that were measured ranged from 4.9 mm to 8.3 mm, exactly comparable to the range of length of weevils described attacking stressed balsam fir and spruce in eastern Canada (5.0–8.0 mm) (Swaine et al. 1924). In the east, oviposition is confined to the base or lower sections of the bole (Swaine et al. 1924; Belyea 1952a), whereas in the current study observations indicate that attack can occur higher and along much of the length of the tree bole. The seasonal history and timing of emergence vary in the literature (Swaine et al. 1924; Belyea 1952a), as they do in this study, with adults emerging from June through August. Observations of this weevil in eastern spruce–balsam fir forests suggest that the insect mainly breeds in severely defoliated and nearly dead trees but are also able to attack trees that have recovered from defoliation events (Belyea 1952b). Host selection parameters appear to be similar on subalpine fir in B.C.; however, the stress level of trees and causal agents of that stress are less obvious.

*Pissodes striatulus* is a large *Pissodes*, with adults averaging 2.6 mm × 6.7 mm (width × length). Late-instar weevil larvae are larger than are bark beetle larvae associated with the phloem of dying subalpine fir and so are easily distinguished. The measurement of *P. striatulus* larval head-capulse widths did not clearly delineate instar separation. There appeared to be four instars, averaging in size from 0.5 mm (first instar) to 1.6 mm (fourth instar). Finding and collecting early instar larvae of this weevil was difficult due to the cryptic nature of attack and oviposition by adults. Adult weevils are difficult to see on tree bark, and the only visible sign of oviposition is a minute resin droplet. Our frequent and rigorous field assessments allowed us to locate several trees undergoing mass attack. However, dissecting out eggs and early instar larvae was difficult. Therefore, early instars were underrepresented in our sampling. Some size distinction occurred among later-instar head-capulse measurements, with a large range in size. Much variation in the size of weevils and their brood occurred, due to parental characteristics (large vs. small mothers), oviposition location on tree bole, age and size of host tree, physiological condition of tree, and other biotic and abiotic influences; thus, the size range of head capsules of successive instars overlaps. Most terminal-infesting *Pissodes* have been reported as having four larval instars (Wallace and Sullivan 1985; Park and Byun 1988; Langor and Williams 1998). Zhang et al. (2004) describe *Pissodes yunnanensis* Langor et Zhang, a weevil that attacks boles of young Yunnan pine, *Pinus yunnanensis* Franchet (Pinaceae), in southwestern China, as having four instars and the head capsule width of the fourth instar averaging 6.1 mm. Finnegan (1958) reported that *P. approximatus* (subsequently shown to be a synonym of *P. nemorensis*) (Godwin et al. 1982; Williams and Langor 2002) has four larval instars with head capsule widths ranging in size from just over 0.3 mm to over 1.4 mm. Reports differ on the number of larval instars of *P. strobi*; Harman (1970) describes five larval instars, with the average head-capulse width ranging from 0.3 mm to 1.2 mm, whereas McIntosh et al. (1996) report four larval instars, with a similar range in average head-capulse width as Harman (1970) from first through final instar.

In summary, *P. striatulus* is capable of mass attacking and killing large, mature subalpine fir trees. Due to its abundance in lower-elevation subalpine fir stands, which experience more frequent and severe drought events, we hypothesise that this abiotic stress on the host tree attracts the weevil. Our findings show that adult weevils overwinter, are likely long-lived, and are capable of oviposition over multiple years, similar to other *Pissodes* species (McMullen and Condrashoff 1973; Furniss and Carolin 1977; Maclauchlan 1992). This would enable *P. striatulus* to take advantage of periodic stressor events such as drought to build up populations rapidly. As moisture stress and higher annual temperatures become prevalent in subalpine fir forests in B.C., the presence and tree-killing habit of *P. striatulus* are likely to increase.
<table>
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<th>Location</th>
<th>Total</th>
<th>1st attack</th>
<th>2nd attack</th>
<th>No. BI with 1st attack</th>
<th>No. BI with 2nd attack</th>
<th>No. BI with WBB</th>
<th>No. BI with sampled WBB</th>
<th>Elevation (m)</th>
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Table 3. Survey results for *Streblus* showing geographic location, with general latitude and longitude (Table Long), elevation, and number of observations.
*Pissodes striatulus* is also found in trees under attack by WBBB, where it may encounter less host resistance. Common tree defence mechanisms such as increased resin flow and the production of defensive chemicals due to insect attack (Berryman and Ashraf 1970; Alfaro *et al.* 2002) would be reduced if WBBB has already mass attacked the tree, making it easier for the weevil to colonise unused portions of the bole. The ability of *P. striatulus* to switch from secondary to primary invader depending upon climate and the host conditions available makes it well suited to adapt to warmer and more severe climate conditions. Subalpine fir is intolerant of high temperatures or moisture deficits (Alexander 1987); therefore, as changes in climate continue, elevated stress levels will continue in these outlying populations of subalpine fir, and potentially in northern and high-elevation forests throughout B.C. Changing climatic conditions, coupled with the fact that adult weevils are long-lived and may have multiple broods, could allow the weevil to proliferate, colonise, and kill an increasing number of trees throughout the range of subalpine fir, accelerating mortality and rates of succession. This study emphasises the need for additional monitoring of and research into high-elevation forests, their insect complexes, and how climate change can impact these fragile relationships.

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**REFERENCES**


