Temperature requirements for western balsam bark beetle (*Dryocoetes confusus* Swaine (Coleoptera: Curculionidae: Scolytinae) development in southern British Columbia

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ABSTRACT

The western balsam bark beetle, Dryocoetes confusus, is the primary biotic disturbance that is causing accelerated subalpine fir mortality in northern and high-elevation forests in southern British Columbia, Canada. The province's climate has warmed dramatically over recent decades and is affecting many biological processes, including those of D. confusus and its host, subalpine fir, Abies lasiocarpa (Pinaceae). Dryocoetes confusus generally undergoes a two-year life cycle, with larvae and teneral adults each overwintering once. To determine whether a univoltine life cycle would be possible, we reared D. confusus from field- and laboratory-infested logs under five constant temperature regimes between 18 °C and 24 °C, with and without cold treatments. Under the coolest regime (18 °C), insect development was arrested in the late larval stage, indicating that an environmental cue is needed for development to proceed or not. At temperatures higher than 21 °C, D. confusus displayed continuous development to teneral adulthood and emergence without requiring a cold period. Our results demonstrate that D. confusus does not have an obligatory diapause, requires 1200 degree-days to complete development, and under warming field conditions, the beetle may be able to switch to a univoltine life cycle. A life cycle contraction could have enormous implications to the future health of subalpine fir forests.

INTRODUCTION

The western balsam bark beetle, *Dryocoetes confusus* Swaine (Coleoptera: Curculionidae: Scolytinae), together with a bluestain fungus, *Grosmannia dryocoetidis* (Ophiostomataceae) (Molnar 1965), is the most destructive insect pest of mature and over-mature subalpine fir, *Abies lasiocarpa* (Hooker) Nuttall in British Columbia (B.C.), Canada (Garbutt 1992), causing scattered yet significant cumulative mortality over large areas of high-elevation and northern forests (Maclauchlan 2016; Maclauchlan *et al.* 2023). This mortality has increased in recent decades and is often referred to as "subalpine fir decline," where abiotic as well as biotic influences affect overall forest health (Reich *et al.* 2016; Lalande *et al.* 2020; Harvey *et al.* 2021; Howe *et al.* 2022).

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Subalpine fir grows well at elevations between 600 and 2500 metres throughout the B.C. Interior and is often found with interior spruce, *Picea engelmannii × glauca* Parry ex Engelmann (Pinaceae) and, to a lesser extent, with other tree species. Subalpine fir occupies the Engelmann Spruce–Subalpine Fir (ESSF) biogeoclimatic zone in B.C. (Lloyd *et al.* 1990; Meidinger and Pojar 1991; Coupé *et al.* 1991). The winters are cold, with significant snowpack, and the summers are cool (Parish and Thomson 1994), and temperatures range from below –45 °C in the winter to above 32 °C in the summer (Alexander *et al.* 2004). Both subalpine fir and interior spruce are shade tolerant, are capable of surviving beneath the canopy of mature trees and are able to take advantage of any gaps created when larger stems die and fall (Klinka *et al.* 2000).

Dryocoetes confusus primarily attacks mature and over-mature subalpine fir in stands aged 100 years or older (Maclauchlan 2016; Maclauchlan *et al.* 2023). The largest diameter subalpine fir in susceptible stands are selected first, although the average diameter of attacked trees can vary widely (Bleiker *et al.* 2003; Maclauchlan and Brooks 2021). Host trees are typically slower growing and sometimes stressed (Bleiker *et al.* 2003). Given the current trends of a warming and drying climate in northern ecosystems (Zhang *et al.* 2019), host trees are likely to become more susceptible to *D. confusus* attack, and the impact of this insect is likely to become more severe. Long-term studies in subalpine fir forests have documented high levels of mortality caused by *D. confusus* (Smith *et al.* 2015), sometimes reaching in-stand mortality rates as high as 80% (Maclauchlan *et al.* 2023).

The life cycle of *D. confusus* in the field generally comprises two years, with the main adult flight occurring between mid-June and mid-July as in-stand temperatures reach 15 °C (Mathers 1931; Stock 1991; Hansen 1996). A second, smaller flight, dominated by parent female beetles, occurs in August–September, with little or no flight between flight periods (Stock 1991; Hansen 1996; Gibson *et al.* 1997; McMillin *et al.* 2001; Negrón and Popp 2009; Stock *et al.* 2013). The second flight may be absent or very small at cooler sites or during cooler summers (Hansen 1996; Gibson *et al.* 1997). Adult beetles are active under the bark long before ambient temperatures trigger emergence and flight (Maclauchlan and Brooks 2017). Pioneering males initiate attack on susceptible subalpine fir, producing pheromones that attract other males and females (Stock and Borden 1983). The beetles transport *G. dryocoetidis* spores externally in mycangia, and the fungus is inoculated into the new host. Initial beetle attacks may be pitched out, but with the introduction of the fungus, the tree can be weakened, which in turn facilitates successful subsequent attack by the beetle. Coalescing lesions caused by the fungus may also girdle and kill trees without further beetle activity (Garbutt 1992).

Males are polygamous, mating with 3–7 females that excavate egg galleries, which radiate from the central nuptial chamber. Parent beetles and late-instar larvae overwinter in the host. The following spring, females may extend their egg galleries and lay additional eggs before both sexes emerge and establish another brood in a new host (Mathers 1931). Teneral adults overwinter (Mathers 1931) and emerge the following summer, thus completing the life cycle in two years. With high-elevation ecosystems experiencing longer periods of warm weather during spring and summer, it is possible that *D. confusus* could shorten its life cycle to one year. As long ago as 1963, Bright conjectured that this might

be possible, especially in the southwestern United States of America. A more recent study by Maclauchlan *et al.* (2023), in which *D. confusus* development in the field was followed for up to six consecutive years, found evidence of a one-year cycle. It is unclear if a larval or adult diapause is necessary to complete development. Spruce beetle, *Dendroctonus rufipennis* Kirby (Coleoptera: Curculionidae: Scolytinae), will successfully complete its life cycle in one year, given appropriate climatic conditions (Hansen and Bentz 2003; Bleiker and Meyers 2017; Bleiker and Willsey 2020). Hansen *et al.* (2011) found that temperature plays a role in spruce beetle diapause induction independent of photoperiod.

Insects, including bark beetles, rely on environmental cues to optimise their fitness. The most probable and important signals for *D. confusus* are likely temperature and moisture because these beetles spend the majority of their lives in the subcortical tissue of subalpine firs. There could be broad ecological and economic implications at both temporal and spatial scales if *D. confusus* were able to compress its life cycle into a univoltine regime. Extrapolating *D. confusus* degree-day (thermoregulation) requirements with known host susceptibility would allow forest managers to adapt and calibrate stand-level models to simulate the effects of projected future climate change on stand development and *D. confusus* susceptibility.

Climate is significantly affecting B.C. and North American forests, as evidenced by the mountain pine beetle, *Dendroctonus ponderosae*, Hopkins (Coleoptera: Curculionidae: Scolytinae), outbreak of 2000–2015 that significantly altered forest landscapes throughout the Pacific Northwest (Kurz *et al.* 2008; Woods *et al.* 2010; Dhar *et al.* 2016; Westfall and Ebata 2017). *Dryocoetes confusus* has also caused significant cumulative mortality over vast areas of forest in B.C. and throughout the species' range (McMillin *et al.* 2003; Lalande *et al.* 2020; Howe *et al.* 2022; Maclauchlan *et al.* 2023). Canada, and northern B.C. in particular, is warming at more than twice the rate of the world's average warming rate (Environment Canada 2022), and drought- and heat-induced tree mortality is accelerating in many forest ecosystems globally. Northern B.C.'s climate has changed dramatically over the past century, with 2 °C of warming recorded during the 20th century. Projections suggest B.C.'s Skeena Region, which has abundant subalpine fir forests, may warm an additional 1.5–4.3 °C by the end of the current century: adapting forest management to address climate change is necessary and must include a full understanding of the biological processes of damaging factors such as *D. confusus*. Better understanding the quiescent or diapause-related developmental delays in *D. confusus* is therefore critical to predicting population pulses in response to changing climate conditions.

We examined the relationship between temperature and growth and developmental rates of *D. confusus* under controlled laboratory conditions to complement a study on *D. confusus* development in the field (Maclauchlan and Brooks 2017). We also investigated the effect of having a cold period at the third larval–instar and teneral-adult stages, which are the overwintering stages commonly encountered in the field, and how this might affect development. This study will enhance our understanding of the life history of *D. confusus* and its ability to respond to rapid and dynamic changes in its environment. If *D.*

confusus has no obligatory diapause, it could readily adapt to warming climates and stressed host conditions and assume a univoltine life history.

The objective of this study was to investigate, by determining the insect's degree-day developmental requirements, whether *D. confusus* can switch to a univoltine life cycle. We also investigated the effect on development and adult emergence of a cold period at key points in the beetle's life cycle.

METHODS

Field collections and rearing

Infested and uninfested subalpine fir was collected from several locations for use in this study, beginning in 1998, continuing through 1999–2000, and in 2014–2015 (Table 1). The uninfested subalpine fir was used as host material for beetles emerging from infested bolts containing late-stage *D. confusus*. The life stages of *D. confusus* within infested subalpine fir used in the controlled temperature rearing studies are listed below:

1. Year 1 – newly infested (field or laboratory) subalpine fir containing eggs and early- to mid-instar larvae in the phloem;
2. Year 2 – infested subalpine fir (brood has overwintered once in the field as larvae) displaying red foliage and containing late-instar larvae, pupae and possibly teneral (new) adults in the phloem; and,
3. Year 3 – infested subalpine fir with dull red foliage (brood has overwintered twice in the field — once as larvae and once as teneral adults) containing overwintered new adults in the phloem.

Some field collections of Year 1 or Year 2 naturally infested or baited subalpine fir were also placed directly into environment chambers for rearing and sampling.

Table 1. Geographic location, latitude, longitude, elevation, and Biogeoclimatic Ecosystem Classification (BEC) of the collection sites for infested and green subalpine fir used in this study. Biogeoclimatic Ecosystem Classification zones are Engelmann Spruce–Subalpine Fir Wet Cold (ESSFwc) and Montane Spruce Dry Mild (MSdm).

Geographic location	Latitude/longitude	Elevation (m)	BEC
Sicamous Research Area	50° 49' 47.13" N, 118° 49' 51.19" W	1600	ESSFwc
Cherry Ridge	50° 18' 33.51" N, 118° 29' 8.74" W	1650	ESSFwc
Spahats Creek Forest Service Road	51° 46' 25.18" N, 119°45' 26.77" W	1600	ESSFwc
Watching Creek	50° 54' 23.64" N, 120° 26' 32.78" W	1375	MSdm
Antler Road	50° 52' 54.12" N, 120° 24' 39.96" W	1260	MSdm

Collections were made from locations where other short- and long-term studies on *D. confusus* were conducted (Maclauchlan and Brooks 2017, 2020, 2021; Maclauchlan *et al.* 2023; Table 1) to maximise the use of staff time in accessing these remote sites. Year 1–3 attack trees and uninfested trees at collection sites were identified, marked, felled, and cut into approximately 45- to 50-cm lengths. Uninfested trees used in the study were of a similar diameter at breast height and age as the infested trees. Throughout the trial, collections were

made in the spring, summer, or fall, starting in late May (Table 2), depending upon the life stages required for rearing. At the laboratory, the cut ends of bolts were waxed to prevent desiccation. Each bolt was labelled as to the location and date of collection and infestation status (uninfested, Year 1 attack, Year 2 attack, or Year 3 attack). From 1998 to 2000, bolts from both unattacked and infested trees were placed in mesh enclosures at ambient temperature (20 °C) within environment chambers (Conviron E15; Controlled Environments Ltd., Winnipeg, Manitoba, Canada) located at the University College of the Cariboo (now Thompson Rivers University) and Kamloops Agriculture and Agri-food Canada (now closed) to allow new adults to emerge from infested bolts and attack uninfested bolts. Both locations were in Kamloops and were easily accessible for regular monitoring and sampling.

In 2014–2015, we conducted additional rearings to supplement the 1998–2000 rearing data and to determine the effects of a cold period on beetle development. To aid in the collection of Year 1 beetles, uninfested standing or freshly felled trees were baited with pheromones ((±)-*exo*-brevicomin; release rate 0.4mg/24 hours) to attract *D. confusus* to these trees. Once the baited trees were fully infested, they were cut into lengths and transported to the BC Ministry of Forests laboratory in Kamloops. In 2014–2015, three environment chambers (Conviron ATC40; Controlled Environments Ltd.) were used (Fig. 1). All environment chambers were kept dark, and a container of water was placed in each chamber to maintain humidity.

Figure 1. A, Infested subalpine fir bolts in environment chambers; B, sample from infested bolt showing *Dryocoetes confusus* nuptial chamber and egg galleries and chip cocoon created by *Pissodes striatulus* larva (upper right); and C, *D. confusus* larvae.

Table 2. List of controlled temperature–rearing regimes showing Dryocoetes confusus infestation year (Years 1–3); stage of D. confusus in infested bolts when collected from field sites; description of how field-infested bolts were treated — (1) placed directly into environment chambers, or (2) beetles were allowed to emerge and infest new, green uninfested bolts) — and whether a cold treatment was applied.

Temperature and infestation year	Stage of *D. confusus* in infested bolts	Treatment	Cold snap
18 °C rearing			
Year 3	Overwintered new adults	Infested bolts placed with uninfested, bolts until emergence occurred and green bolts were infested	No
20 °C rearing			
Year 1	Eggs–larvae before first overwintering period	Field-infested bolts placed in environment chamber for rearing and assessment	With and without cold snap
Year 3	Overwintered new adults	Infested bolts placed with uninfested bolts until emergence occurred and green bolts were infested	No
21 °C rearing			
Year 1	Eggs–larvae before first overwintering period	Field-infested bolts placed in environment chamber for rearing and assessment	No
Year 3	Overwintered new adults	Infested bolts placed with uninfested bolts until emergence occurred and green bolts were infested.	No
23 °C rearing			
Year 1	Eggs–larvae; before first overwintering period	Field-infested bolts placed in environment chamber for rearing and assessment	No
Year 3	Overwintered new adults	Infested bolts placed with uninfested bolts until emergence occurred and green bolts were infested	No
24 °C rearing			
Year 1	Larvae before first overwintering period	Field-infested bolts placed in environment chamber for rearing and assessment	With and without cold snap
Year 2	Pupae and teneral adults before second overwinter period	Infested bolts placed with uninfested, bolts until emergence occurred and green bolts were infested	No
Year 2	Pupae and teneral adults before second overwinter period	Field-infested bolts placed in environment chamber for rearing and assessment	With and without cold snap

Due to limited space in the environment chambers (Fig. 1) and the length of time required for beetles to complete development, the studies were conducted over five years: from 1998 to 2000 and from 2014 to 2015. Adult *D. confusus* were allowed to emerge naturally from infested bolts and to attack the green, unattacked bolts (Table 2). Beetle activity and attack were observed daily until there was evidence of gallery construction. When sufficient attack had occurred (± 4 females per gallery), the freshly attacked green bolts were placed into the environment chambers, each of which was set at a fixed temperature. The temperature regimes selected for rearing *D. confusus* were 18 °C, 20 °C, 21 °C, 23 °C, and 24 °C. Under the 20 °C and 24 °C temperature regimes (Table 2), Year 1 field-infested bolts were given a 28-day cold period (0–3 °C) when most of the larvae had reached third instar (Table 2) to observe whether insect development was affected by a cold period. Applying this cold period immediately after late-summer field collection mimicked the conditions insects would encounter in the field. We also compared the rearing of Year 1 field-infested bolts (collected in late summer before the onset of the first overwintering period) placed immediately into the 24 °C environment chamber to the bolts given a cold period before being placed in the 24 °C chamber. The rate of development for *D. confusus* life stages reared in field-infested *versus* laboratory-infested material at 24 °C was compared using regression analysis.

Life stage sampling and instar determination

All infested bolts used for rearing in the five temperature regimes were sampled at regular 3- to 4-day intervals. Two 6- to 8-cm^2 bark samples were stripped off a sample bolt in each chamber to expose one complete gallery system (including nuptial and female egg galleries). We recorded the exact day of attack on the green, uninfested bolts that were placed with infested bolts from which new adults were emerging, making it possible to count eggs. Every effort was made to position the bark sample over an entrance hole (Fig. 1). All live individual beetles at each developmental stage were recorded. Under some rearing regimes, exit holes were noted but not counted. Care was taken not to mistake parent adults for new adults and emergence holes made by parent adults for exit holes made by new adults. Exit holes made by parent adults were located directly over a parent egg gallery, and exit holes made by new adults were situated throughout the bark samples. Larvae were stored in 70% ethanol and later measured using a Meiji binocular microscope (Meiji Techno, Saitama, Japan) at 4.5× magnification equipped with an ocular micrometer, which yielded a micrometer measurement of 0.022 mm. Larvae were assigned instars based on the distribution of head-capsule widths (Maclauchlan and Brooks 2017). Measurements were taken across the widest portion of the head capsule in 0.022-mm increments. 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. Under some of the 24 °C rearing regimes, larval instars were assigned by using an ocular micrometer marked with pre-determined larval-instar delineations (Maclauchlan and Brooks 2017).

A representative sub-sample of first- and second-instar larvae were measured when large samples (*i.e.*, ≥ 300 larvae) were taken. Approximately 40 individuals

from each instar were measured at each sampling occasion, and the instar for the remaining larvae was then estimated using the instar delineations (Maclauchlan and Brooks 2017).

Degree-day calculations

Accumulated heat sums, measured in the number of degree-days above a developmental threshold temperature, were determined using the methods of McMullen (1976), Sieben (1996), and Wermelinger and Seifert (1998). We used 6.1 °C as the threshold temperature for development, after Dyer *et al.* (1968), who determined that it was a good baseline temperature for spruce beetle. *Dryocoetes confusus* occupies the same high-elevation forests as spruce beetle; therefore, we also used this temperature as a baseline. Maclauchlan and Brooks (2017) observed that *D. confusus* activity under the bark began when minimum daily phloem temperatures reached or exceeded 5 °C, before emergence and flight initiation, which occurred at higher phloem temperatures. Therefore, using 6.1 °C as the threshold temperature for *D. confusus* is conservative. Johansson *et al.* (1994) used 7.1 °C and 7.9 °C as the threshold temperatures for various life stages of *Dryocoetes autographus* (Coleoptera: Curculionidae: Scolytinae) after Arnold (1959). We calculated the number of days required to obtain 50% of each developmental stage under each temperature regime. This was determined by interpolation between the two points closest to 50%. Where possible, this was also done for the egg-laying stage, which was then added to the time for 50% occurrence in the regime. The degree-day requirements for each life stage were calculated using the number of days at each temperature regime multiplied by the rearing temperature (T_r) minus the developmental threshold temperature (T_d): number of days at T_r [$T_r - T_d$] (Zar 1984; McIntosh and McLean 1997).

K. Bleiker and J. Thain (Natural Resources Canada, Pacific Forestry Centre, Victoria, B.C.) generated daily minimum, maximum, and mean air temperatures for five study sites in the B.C. Southern Interior using BioSIM, version 11. The average heat sums over the lower developmental threshold of 6.1 °C (Dyer *et al.* 1968; Dyer and Hall 1977) were calculated using 2021 data from the mean of 50 simulations (Régnière 1996; Bleiker and Willsey 2020). BioSIM spatially interpolates temperature data from the eight nearest Environment Canada monitoring stations and adjusts for distance and elevation. The five sites were Sicamous Creek, Cherry Ridge, and Spahats Creek, where *D. confusus* was collected for this study, and two additional lower-elevation sites where *D. confusus* occurs (Antler Road and Watching Creek; Maclauchlan and Brooks 2020).

RESULTS

Dryocoetes confusus does not have an obligatory diapause (Fig. 2). In both field- and laboratory-infested bolts, reared-from-egg or early-instar larvae showed continuous development through to teneral adults and emergence as new adults (Table 3). In addition, when field-infested bolts containing Year 2 brood (late-instar larvae, pupae, and teneral adults) were brought into the laboratory before the second field-overwintering period as adults, insects completed development to teneral adults, emerged as new adults, and were able to successfully attack green, uninfested bolts (Table 3). This demonstrates that

teneral adults in the field-collected material (Year 2) did not have an obligatory diapause in the adult stage. Therefore, a switch to a univoltine life cycle is possible if sufficient degree-day accumulation occurs in the field.
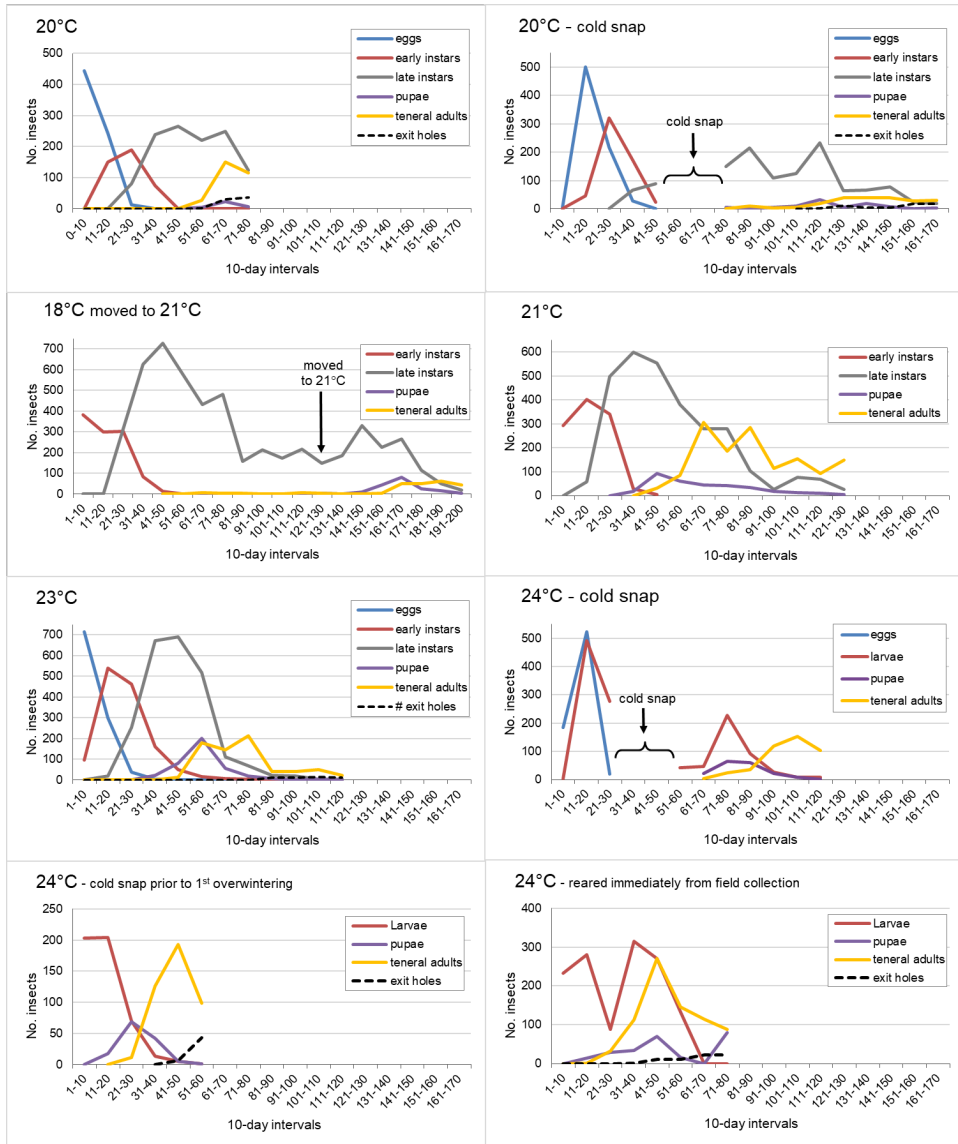

Figure 2. Life stage development of *Dryocoetes confusus* at five temperature rearing regimes, with and without a cold snap (labelled on graph). Samples were excised at 3- to 4-day intervals from bolts in five temperature regimes to determine life stages present. Rearing data at the same temperature receiving the same treatment (with or without a cold snap) were combined into one graph. Some sampling commenced when the egg stage was no longer present.

Table 3. Summary of the number of *Dryocoetes confusus* life stages recorded at five temperature regimes, showing the stage of beetles collected from the field (Years 1–3 and life stage) and treatment regime applied. The treatment regime indicates whether field collections were allowed to emerge and infest new, green host material or whether they were placed immediately in an environment chamber for rearing. Treatment regime 1: infested bolts placed with uninfested, bolts until emergence occurred and green bolts were infested; Treatment regime 2: field-infested bolts placed in environment chamber for rearing and assessment.

Temp. (°C)	Field-infestation stage	Treatment regime	No. rearing days	Eggs	Early instars	Late instars	Pupae	Teneral adults	Exit holes	Total no. life stages
18	Year 3; new adults	1	129		1088	4071	13	20		5192
18–21	Year 3; new adults	1	129 + 70			1192	182	214		1588
20	Year 3; new adults	1	66	715	418	1113	21	16		2283
20	Year 1; later-instar larvae	2	80			65	14	277	70	426
20	Year 1; eggs, larvae	2	147	755	563	1236	89	217		2920
20	Year 3; new adults	1	129		1071	2949	342	1403	60	5765
21	Year 3; new adults	1	84	395	673	1719	253	417	17	3474
23	Year 1; eggs, larvae	2	123	661	678	685	146	294	56	2520
23	Year 2; pupae, tenerals	1	63		279	743	80	58		1160
24	Year 3; new adults	1	110	728	614	614	186	486		2628
24	Year 1; later-instar larvae	2	81		59	238	86	650	71	1104
24	Year 1; later-instar larvae	2	59		92	404	135	429	49	1109
24	Year 2; pupae, teneral adults	2	44			3	105	58	58	224
24	Year 2; pupae, teneral adults	2	27			3	142	47	48	240
				3254	**5535**	**15 103**	**1852**	**4684**	**459**	**30 887**

In total, more than 30 000 life stages were recorded during the bolt dissections (Table 3). Development was further advanced in the Year 1 fall field collections, so no eggs were collected for that group, whereas Year 1 field collections made in early summer contained eggs and early-instar larvae. Larvae comprised the largest proportion of life stages dissected from the bolts, approximately 61% of all life stages found (Table 3).

Cut-off points for larval instars were assigned based on 15 331 head-capsule measurements (Table 4). Head-capsule widths ranged from 0.308 mm to 1.035 mm. Three distinct larval instars were observed at the cooler temperatures (18 °C and 20 °C). Under the warmer temperature regimes (21–24 °C), a fourth instar appeared or, more likely, there was a bimodal third-instar distribution (Floater 1996). Stock (1981) reported a similar distribution pattern in laboratory rearing experiments, using field-collected green subalpine fir bolts kept at 24 °C. Larval samples collected under field conditions do not exhibit this third-instar bimodal distribution (Maclauchlan and Brooks 2017).

Table 4. Head-capsule width and larval-instar designation for laboratory-reared *Dryocoetes confusus* measured in 1998 and 1999.

Larval instar	Head-capsule width (mm)
1	0.308–0.418
2	0.440–0.638
3	0.660–0.899
4	> 0.90 or possible bimodal third instar

At each temperature, *D. confusus* development followed a similar pattern, beginning with many eggs at the onset, followed by a steady increase of early-instar larvae (Fig. 2). At around 30 days, late-instar larvae appeared. At this point, whether the insects continued to develop depended on the regime temperature. At 18 °C, larvae reached the third-instar stage, and then development ceased until the bolts were placed at 21 °C to observe whether the insects would continue to develop. After just 10 days at 21 °C, adult beetles began to emerge (Fig. 2). For bolts placed in the 21 °C chamber at the onset of the trial, adult emergence occurred between 50 and 120 days (Fig. 2). Although the insects developed through to adults at 20 °C with or without a cold snap, not many were successful, and most remained as larvae. Whereas under the 21 °C, 23 °C, and 24 °C regimes, continuous development was observed from larvae through to pupae, adults, and emergence (Fig. 2) without this "stalling" of development. The rate of *D. confusus* development in field-infested or laboratory-infested material did not differ when the insects were reared at 24 °C ($R^2 = 0.7$). The number of larvae reared under the 18 °C and 20 °C regimes peaked at 40–50 days. Larval numbers peaked at about 40 days in temperatures 21 °C and higher. Teneral adults and emergence occurred between 60 and 80 days in the 20 °C environment chamber and at 40 days and beyond in the 23 °C chamber (Fig. 2). At 20 °C and 24 °C, a cold period was introduced once the majority of the insects had reached the third instar. Thereafter, when development recommenced, it was clear once again that 20 °C was not an ideal temperature for successful development. The insects reared at cooler

temperatures, below 21 °C, took more days to complete development and produced far fewer adults.

The total number of larvae measured per rearing regime ranged from 297 to 5155 (average ± standard error: 1864 ± 448) larvae (Table 3; Fig. 3). *Dryocoetes confusus* spends the largest proportion of total development time as third-instar larvae (Fig. 3).
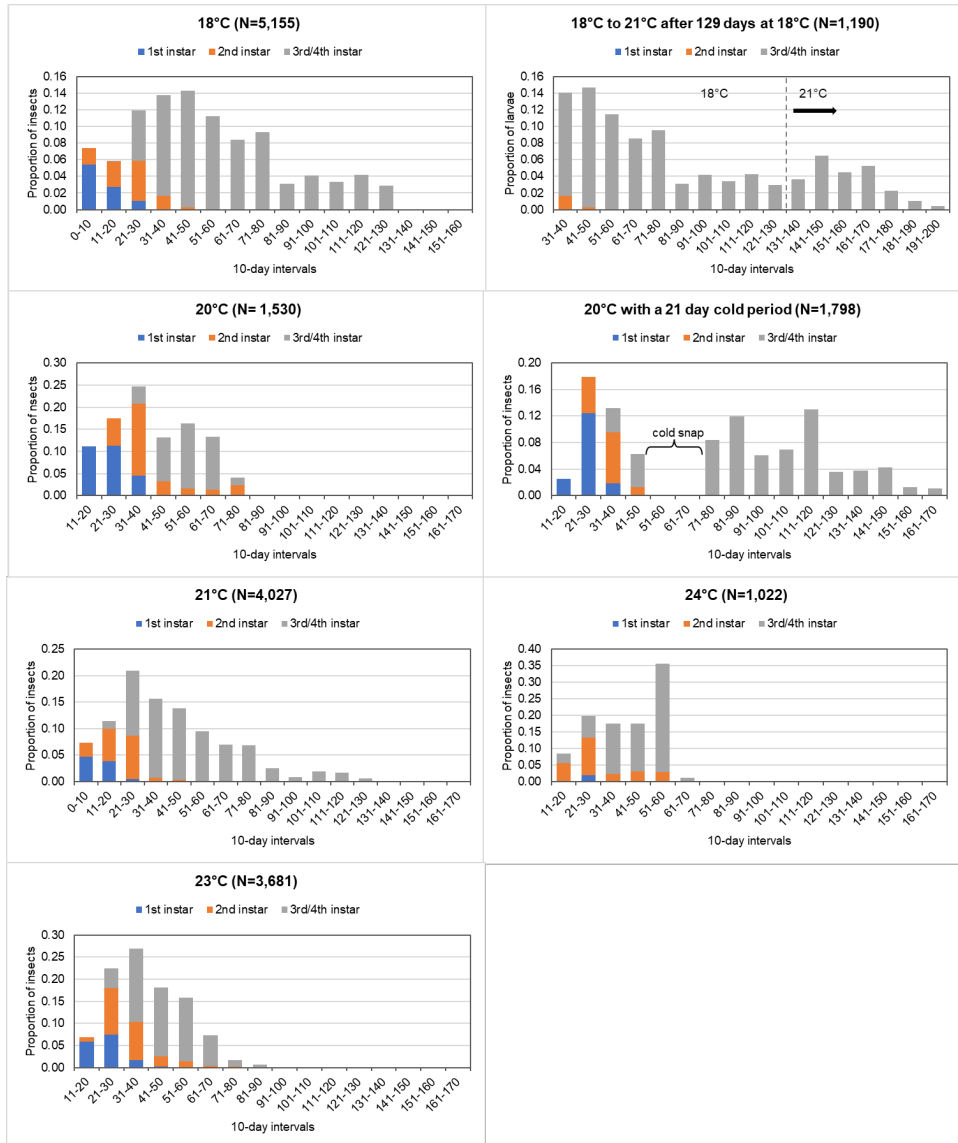

Figure 3. Frequency distribution of *Dryocoetes confusus* larval instars reared at five temperatures, by 10-day intervals. Rearing data at the same temperature receiving the same treatment (with or without a cold snap) were combined into one graph.

We calculated the number of days required to obtain 50% of each larval instar at several rearing temperatures. At 18 °C and 21 °C, approximately 10 days were necessary for the first instar, whereas at higher rearing temperatures, approximately 20 days were required for the insects to reach the first instar. The same pattern was observed for second-instar larvae, with approximately 20 days required at 18 °C and 21 °C and 30 days at 23 °C. However, under the 24 °C regime, just over 20 days were needed, similar to the 18 °C and 21 °C regime. Under the 18 °C regime, third-instar larvae "stalled" and did not continue developing until the bolts were moved to the 21 °C chamber. Under other temperature regimes, third-instar larvae continued to develop. The number of days required to obtain 50% of the third instar at each regime was similar (Fig. 4), ranging from 44 to 52 days.
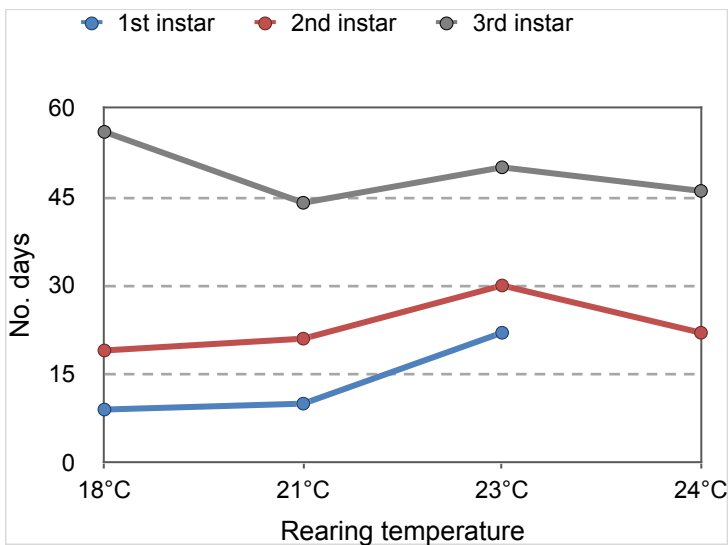

Figure 4. Number of days required for 50% of each *Dryocoetes confusus* larval instar at four temperature rearing regimes.

Dryocoetes confusus eggs are laid over a short and discrete period once adult beetles have mated. Due to this short timeline and because eggs are small and difficult to see and count, this is a challenging life stage to accurately record and assess. When the insects had reached the pupae and teneral adult stages, the number of degree-days had evened out across the rearing temperatures (Table 5). Two rearing regimes were given a cold period (21 to 28 days) when the majority of the larvae were late instars (Table 5). After the cold periods had ended, insects being reared under the 24 °C regime developed rapidly, with third-instar larvae successfully pupating and many individuals becoming adults. The opposite was recorded for the 20 °C rearing regime, where after the cold snap, insects did not develop rapidly or move into the next stages of development. Although both rearing regimes had similar numbers of eggs and larvae dissected during the pre-cold period, once the cold period had elapsed, larvae remained stalled in the 20 °C rearing regime (Table 5; Fig. 2), indicating that at or below 20 °C, *D. confusus* continues development but may need a climatic trigger to halt or advance development more rapidly. Maclauchlan and Brooks (2017) found that

minimum daily phloem temperatures of at least 5 °C and maximum daily phloem temperatures of at least 20 °C initiated emergence and flight. The average number of degree-days for 50% of the population to reach each life stage (above 6.1 °C) over all rearing regimes was 133.3 ± 14.8 for eggs; 608.4 ± 79.9 for larvae; 984.1 ± 60.8 for pupae; and 1187.6 ± 63.7 for teneral adults (Fig. 5).

Table 5. Calculated degree-days required for each life stage of *Dryocoetes confusus* reared at one of five temperature regimes.

Rearing temperature	Life stage	N	Range of days	No. of days for 50% development	Calculated degree-days[1]
18 °C	Eggs	Not counted	0–21	10	119
20 °C		715	0–27	9	125
21 °C		Not counted	7–13	10	139
23 °C		395	3–22	10	169
23 °C		661	0–22	6	101
18 °C	Larvae	6756	0–129	38	452
20 °C		1543	12–84	41	570
21 °C		4952	7–129	27	402
23 °C		2370	12–89	43	727
23 °C		1324	0–74	25	423
18 °C	Pupae	13	59–129	105	1250
20 °C		21	69	69	959
21 °C		342	35–122	60	894
23 °C		253	41–86	54	913
23 °C		146	44–109	57	963
18 °C	Teneral adults	20	59–129	84	1000
20 °C		16	69	69	959
21 °C		1403	45–129	83	1237
23 °C		417	49–87	69	1166
23 °C		294	49–123	80	1352
24 °C	Eggs	718	0–17	11	197
	Larvae	774	3–25	12	215
Cold for 28 days					
	Larvae	417	53–84	39	698
	Pupae	158	62–84	43	770
	Teneral adults	491	62–110	66	1181
20 °C	Eggs	749	0–22	6	83
	Larvae	717	3–40	17	236
Cold for 21 days					
	Larvae	1082	53–150	71	987
	Pupae	89	65–150	82	1140
	Teneral adults	217	76–150	102	1418

[1]6.1 °C used as the threshold temperature to calculate degree-days (Dyer *et al.* 1968).
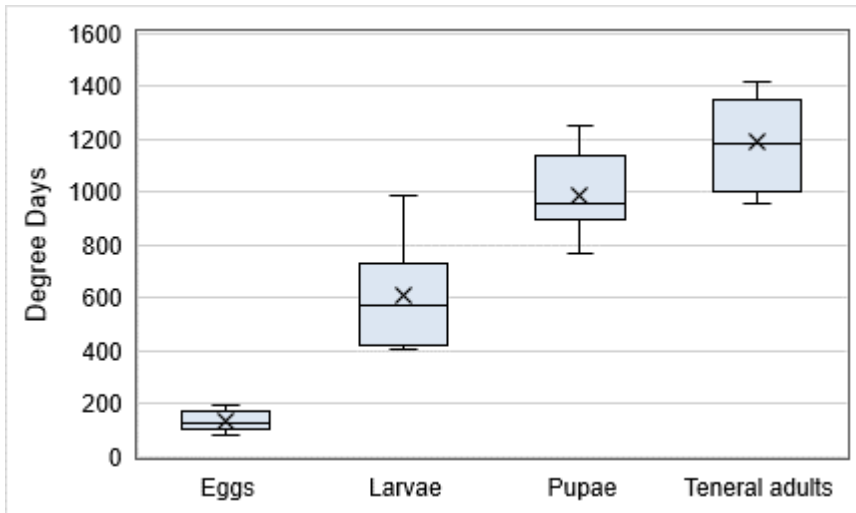
Figure 5. The mean and median number of degree-days required (all five temperature regimes combined) by Dryocoetes confusus for 50% of the population to reach each life stage (above 6.1 °C; × = mean; line = median).

Dryocoetes confusus that were field collected before their second overwintering period and reared at 24 °C with and without a cold period (0–3 °C) before being placed in the 24 °C environment chamber exhibited similar development trends. The life stages under the bark were comprised primarily of teneral adults, with very few late-instar larvae or pupae (Table 6). A secondary flight sometimes occurs in late August or early September (Maclauchlan and Brooks 2017), so adults were still active. Based on available weather data, the average daily temperatures would not yet have reached a point where all development would have ceased. Fifty-eight exit holes were counted, and 51 adults emerged within 38 days of being placed in the 24 °C environment chamber. In contrast, the bolts given a cold snap before being placed at 24 °C took only 27 days to emerge (Table 6). These adults were then observed boring into logs.

Table 6. The number of *Dryocoetes confusus* dissected from Year 2 field-infested bolts brought into the laboratory in September 2014 and either immediately placed at 24 °C or given a cold period (0–3 °C) until January 2015, then placed at 24 °C.

10-day intervals	24 °C no cold			24 °C cold snap		
	Late instars	Teneral adults	Exit holes	Late instars	Teneral adults	Exit holes
1–10	0	15	4	3	73	11
11–20	3	27	3	0	63	16
21–30	0	25	18		6	20
31–40		33	26			
41–50		5	7			
Totals	**3**	**105**	**58**	**3**	**142**	**47**

Insects developed successfully through to adult and then emerged from the bolts without requiring a cold period. A cold period did not deter or impede further development when that period ended. The calculated heat sums over 6.1 °C at each site ranged from 769 degree-days at Spahats Creek to 1151 degree-days at Antler Road, the lowest-elevation site (Table 7).

Table 7. Heat sums available at five sites in the B.C. Southern Interior (generated by K. Bleiker and J. Thain, Natural Resources Canada, Pacific Forestry Centre, Victoria, B.C., using BioSIM, version 11K).

Location	Elevation (m)	Available heat sums (2021)
Antler Road	1260	1151
Watching Creek	1375	1017
Spahats Creek FSR	1600	769
Sicamous research area	1600	948
Cherry Ridge	1650	965

DISCUSSION

This study has clearly demonstrated that *D. confusus* does not have an obligatory diapause and, given suitable field conditions, could switch to a univoltine life cycle at some sites. Under all but the coolest 18 °C rearing regime, *D. confusus* displayed continuous development from egg to teneral adult and adult emergence. The lower number of degree-days required to complete development at 18 °C and 21 °C was mostly likely because very few individuals made it to adulthood (Table 5) and is therefore not representative. In the coolest regime, very little development occurred beyond the larval stage, indicating that insects were slowing their metabolic processes, possibly entering a quiescent or facultative diapause state, and requiring either a warmer temperature cue to continue development or, conversely, colder temperatures to arrest development. The capacity for diapause or some form of dormant state enables insects to survive seasonal environments (Denlinger 2023), such as severely cold winter temperatures in the case of *D. confusus*. At the present study's cooler rearing regimes, 18 °C and 20 °C, insects developed through the first and second instars more rapidly than they did at the warmer temperature regimes, which suggests that these early developmental stages have evolved to this condition and that either warmer conditions are less conducive or the habitat becomes suboptimal. In natural field situations, adult emergence and flight generally commences when subcortical temperatures exceed daily minimum temperatures of 5 °C and daily maximum temperatures of 20 °C (Maclauchlan and Brooks 2017). However, adult brood gallery construction and egg laying under the bark can commence as early as April (Maclauchlan and Brooks 2017), which suggests that even cooler daily temperatures may be sufficient for physiological development and activity. That said, when insects developing in the 20 °C temperature regime in the present study were given a cold-period treatment at the third-instar stage, they displayed a slowed and prolonged development that may indicate they were emerging from a diapausal state.

Field studies of *D. confusus* commonly report three larval instars (Negrón and Popp 2009; Maclauchlan and Brooks 2017); but under the warmer rearing regimes in the present study, we found evidence of a bimodal third or possibly

fourth instar. Temperature and humidity — particularly low humidity — may change and lessen the quality of the environment in which insects are developing, thereby affecting instar (Esperk *et al.* 2007). This bimodal third or fourth instar may serve as a compensatory mechanism to achieve a threshold size in less than optimal conditions.

Late-instar larvae and teneral adults brought in from the field before the onset of cold weather successfully emerged whether they were given a cold treatment or not before being placement in a 24 °C environment chamber. Insects subjected to a cold treatment emerged slightly faster than those that did not receive a cold treatment, but the difference in timing was minimal. Spruce beetle has exhibited a strong response to cold treatment (Bleiker and Willsey 2020), having a slow and protracted emergence in the absence of a substantive cold period, thereby indicating an obligate diapause for adults. More work is necessary to determine the temperature requirements and response of new adult *D. confusus* pre-emergence and their physiological state post-emergence.

Dryocoetes confusus is described as semivoltine, completing its development in two years (Mathers 1931; Bright 1963; Stock 1991); however, our data suggest that under more favourable climatic conditions, the insect may be able to switch to a univoltine cycle. Bright (1963) thought *D. confusus* displayed a one-year life cycle in the western United States of America, which has a warmer climate than the insect's northern range in B.C., and Maclauchlan *et al.* (2023) saw evidence of a one-year life cycle in their long-term field studies in southern B.C. During the late, second seasonal flight, male and female *D. confusus* can colonise a suitable host, often using hosts attacked previously during the first seasonal flight and construct a nuptial chamber (or hibernation chamber; Bright 1963) under the bark in which parent beetles overwinter. This strategy optimises parent beetles' ability to initiate brood gallery construction and egg laying very early the following spring and to benefit from the maximum number of growing degree-days available. In addition, the extension of brood galleries and egg laying in the second year by overwintered females in existing egg galleries (Bright 1963; Garbutt 1992) extends the growing degree-days available to brood.

Timing of the first and second seasonal flights varies depending on geographic area, elevation, and annual climatic conditions (Hansen 1996; Negrón and Popp 2009; Stock *et al.* 2013; Maclauchlan and Brooks 2017), thereby allowing for considerable developmental flexibility. With warming temperatures and heat or drought conditions extending into September and October, field conditions may become favourable for *D. confusus* and enable some beetles to switch to a univoltine life cycle.

Dryocoetes confusus can develop from egg to adult and successfully emerge under controlled temperature regimes, provided the temperatures are high enough to trigger development past the late-larval stage. The average physiological and chronological time required for the completion of development was longer for larvae than for eggs, pupae, or teneral adults. On average, larvae required 608 degree-days (above 6.1 °C) for 50% of the population to reach that stage, or in chronological time, about 41 days. Pupae on average required 984 degree-days, a difference of 376 degree-days from larvae, or 32 chronological days. Generally, teneral adults were present within 12 days of the pupal stage, an additional 203 degree-days. However, the developmental thresholds for early-*versus* late-instar larvae and for pupae and adults may differ depending on the

life stage (Wermelinger and Seifert 1998). Historically, the optimal development season is short in the natural habitat of *D. confusus*; however, it may only take a few weeks of warmer weather to influence insect development.

Dryocoetes confusus required slightly less than 1200 degree-days to complete its development when averaged over the five temperature regimes. Bleiker and Willsey (2020) calculated the average annual cumulative number of degree-days over 6.1 °C at two spruce beetle sites in B.C. to be just over 1300. These sites were comparable to sites where subalpine fir and *D. confusus* are found. We calculated the available heat sums above 6.1 °C at five subalpine fir sites based on 2021 weather data to range between 769 and 1151 degree-days. Based on these results, sufficient thermal accumulation could occur for *D. confusus* to exhibit a univoltine life cycle. Annual fluctuations in climate patterns greatly influence the rate and success of insect development and elicit a variety of developmental responses (Bentz *et al.* 2010). *Dryocoetes confusus* develops well in cooler temperatures until the third instar; it then appears to require an environmental cue to proceed or halt development, as evidenced by the 18 °C rearing treatment in the present study. When rearing temperatures were at least 21 °C, the larvae readily developed to adults. Maclauchlan and Brooks (2020) found average daily maximum temperatures in a subalpine fir stand where both *D. confusus* and *Pissodes striatulus* (Coleoptera: Curculionidae) were present to be at least 21 °C for more than two months, at times reaching 30 °C.

This study provides a basis for understanding the physiological development of *D. confusus* and shows where further investigation is warranted — in particular, the determination of potentially different developmental thresholds for each life stage, especially newly emerging adults. We show that adults emerge from Year 2–attacked trees and readily attack green hosts but not whether these beetles can fly and disperse to new hosts. Additional field observations at the start and end of the development season would clarify the onset of oviposition, the function of late-stage attack, and the creation of nuptial (hibernation) chambers in which parent adults overwinter.

This study increases understanding of the life history of *D. confusus* and its ability to respond to rapid and dynamic changes in its environment. Without an obligatory diapause, *D. confusus* can react and adapt to changing environmental and host conditions by shortening its life history. This ability has potentially enormous ecological and economic ramifications in high-elevation and northern subalpine fir forests, which are susceptible to climate change and have been warming at an accelerated rate compared to other ecosystems in B.C. In future years, forest managers must more carefully consider how these delicate ecosystems are managed.

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