



# Influence of temperature on the reproductive success, brood development and brood fitness of the eastern larch beetle *Dendroctonus simplex* LeConte

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- Abstract**
- 1 The eastern larch beetle *Dendroctonus simplex* LeConte colonizes the phloem of tamarack *Larix laricina* (Du Roi) K. Koch, preferring recently dead or moribund trees weakened by insect defoliation or other factors that predispose trees to beetle attack.
  - 2 Outbreaks of eastern larch beetles are typically localized, of short duration, and collapse when the supply of stressed hosts is exhausted. Although rare, landscape-level outbreaks of eastern larch beetles can occur if large areas of tamarack become stressed.
  - 3 From 2000 onward, an ongoing outbreak of eastern larch beetles in the Great Lakes Region of North America has resulted in extensive mortality to more than 75 000 ha of tamarack forest in Minnesota, U.S.A. This outbreak has no known biotic predisposing factor, such as extensive defoliation. Trends of recent climate warming, however, are suspected to be a contributing factor.
  - 4 Current efforts to model the effects of climate on eastern larch beetle population dynamics are hampered by an absence of data relating beetle developmental biology to temperature. In a laboratory study, we studied eastern larch beetle reproductive success, larval development and offspring fitness at temperatures in the range 9.9–29.4 °C.
  - 5 Offspring production was similar across temperatures. Successful brood development occurred at 9.9 °C, whereas the minimum and optimal developmental temperatures were calculated to be 7.5 and 27.9 °C, respectively. Offspring size and lipid content were maximized between 20 and 22 °C.
  - 6 Our results indicate a potential trade-off between temperatures that maximizes eastern larch beetle offspring fitness versus developmental rate. The implications of such a trade-off are discussed with respect to beetle population dynamics.

**Keywords** Bark beetle, climate change, climate warming, developmental rate, developmental threshold, lipid analysis, offspring fitness, reproductive success.

## Introduction

Herbivorous insects represent integral components of forest ecosystems, influencing floral and faunal diversity, water quality, stand age, size and genetic structure, fire regimes, and nutrient cycling (Kurz *et al.*, 2008; Raffa *et al.*, 2008; Hicke *et al.*, 2012). Such landscape-level impacts are frequently tied to dramatic insect population eruptions, which vary in size and extent. Large-scale disturbances from insect outbreaks may be occurring with increasing frequency and severity because the thermal

constraints that affect the population dynamics of many insects are changing (Bale *et al.*, 2002). Indeed, recent changes in climatic patterns have been altering the population dynamics and geographical ranges of several species of forest insects (Bale *et al.*, 2002; Carroll *et al.*, 2004; Aukema *et al.*, 2008; Raffa *et al.*, 2008; Waring *et al.*, 2009).

More frequent outbreaks of bark beetles (Coleoptera: Curculionidae), such as species within the genus *Dendroctonus*, recognized for their economic impacts on forest resource management (Werner *et al.*, 2006; Raffa *et al.*, 2008; Bentz *et al.*, 2010; Sambaraju *et al.*, 2011), have resulted in a widespread increase in forest mortality throughout western North America (Raffa *et al.*, 2008; Bentz *et al.*, 2010). For example, a

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hyper-epidemic of the mountain pine beetle *Dendroctonus ponderosae* Hopkins in western Canada is orders of magnitude larger than previous epidemics (Aukema *et al.*, 2006; Raffa *et al.*, 2008; Alfaro *et al.*, 2010). Moreover, the spruce beetle *Dendroctonus rufipennis* (Kirby) has erupted in areas of western North America (Holsten *et al.*, 1999; Jenkins *et al.*, 2014) coincident with drought conditions (Chapman *et al.*, 2012; Hart *et al.*, 2014) and release from thermal constraints (Berg *et al.*, 2006; Raffa *et al.*, 2008; Bentz *et al.*, 2010; Hansen *et al.*, 2011).

In the Great Lakes Region of North America, an ongoing outbreak of the eastern larch beetle *Dendroctonus simplex* LeConte has resulted in extensive mortality of eastern larch (tamarack) *Larix laricina* (Du Roi) K. Koch forests in Minnesota, U.S.A., from 2000 onward (MNDNR, 2012). Concomitantly, activity has been increasing in Wisconsin and Michigan, U.S.A., as well as in Ontario, and Manitoba, Canada (ONMNR, 2012; MIDNR, 2013; WIDNR, 2013; MBCFB, 2014). Moreover, from 2009 onward, the first recorded outbreaks of eastern larch beetles have been occurring in Alberta, Canada (D. Langor, personal communication). The eastern larch beetle is almost exclusively monophagous on tamarack (Wood, 1982). The distributions of both the eastern larch beetle and tamarack are synonymous across North America from Alaska in the northwest, eastward throughout the boreal forest of Canada and the northern U.S.A., to the Canadian Maritime provinces, and south to the north-eastern U.S.A. (Burns & Honkala, 1990; Seybold *et al.*, 2002). More than 75 000 ha of tamarack forest has been killed by the beetle in Minnesota subsequent to 2000, representing approximately 18% of the tamarack in the state (MNDNR, 2013). This is the third major reported outbreak for this insect, with two large outbreaks occurring concurrently in Alaska (3.3 million ha of tamarack forest affected) and the east coast of North America (>1.4 million m<sup>3</sup> of tamarack killed) in the late 1970s and early 1980s (Werner, 1986; Langor & Raske, 1989a, 1989b). Prior to 1970, no landscape-level outbreaks of eastern larch beetles had been recorded (Langor & Raske, 1989a, 1989b).

Eastern larch beetles typically colonize recently dead tamaracks or those that have been weakened by some stressing agent, such as flooding, cold soils, or insect defoliation (Werner, 1986). Females are the host-selecting sex, releasing aggregation pheromones to attract conspecifics *en masse* to overcome host defences and facilitate reproduction (Prendergast, 1991). Eggs are laid in the phloem within niches that are cut into the margins of the parental galleries. Eclosed larvae create feeding galleries perpendicular to the parental gallery. After laying the first larval brood in the spring, parent beetles may re-emerge from the colonized tree and establish a second and sometimes a third sibling larval brood in additional trees or host material. Larvae develop to adults by mid-summer or autumn. After pupation, some progeny emerge and drop to the base of the tree where they create overwintering galleries, whereas others remain in the pupal chamber throughout the winter (Simpson, 1929; Wood, 1982; Werner, 1986; Langor & Raske, 1987a, 1987b; Seybold *et al.*, 2002). The over-wintering life stage is typically the brood adult, although larvae are more cold tolerant than adult life stages (Venette & Walter, 2008). Brood adults purportedly must over-winter to break a reproductive diapause and become reproductively mature the next spring (Langor & Raske, 1987b), although laboratory data suggest otherwise (McKee & Aukema, 2014).

When environmental conditions permit, rapid population increases of eastern larch beetles may occur. However, outbreaks are typically ephemeral and confined to small, localized areas of moribund trees. Small, localized infestations of eastern larch beetles have been documented for more than 100 years (Hopkins, 1909; Wood, 1982). Infestations of healthy trees are typically short-lived and last only a few years, ending when beetles exhaust the proximate, weakened host supply (Langor & Raske, 1989a, 1989b).

Two attributes make the outbreak of eastern larch beetles in Minnesota unique. First, this is the only landscape-scale outbreak of eastern larch beetles ever recorded in central North America. Second, unlike previous eastern larch beetle outbreaks, the outbreak in Minnesota is not associated with any biological disturbance event (e.g. tamarack defoliation) that would predispose the tamaracks to colonization by eastern larch beetles (Albers, 2010). Although the large outbreaks in Alaska and eastern Canada in the late 1970s and early 1980s were more expansive and pronounced than any previous eastern larch beetle activity, they were associated with prior insect defoliation, localized flooding and general tamarack decline (Werner, 1986; Langor & Raske, 1989a, 1989b). In the absence of a disturbance agent, climatic patterns, such as warming trends in seasonal temperatures, are suspected to be contributing to the beetle outbreak in Minnesota (Venette & Walter, 2008).

Efforts aiming to understand how current climate patterns may be affecting the biology of eastern larch beetles, as well as potential links to outbreak behaviour, have been hampered by a lack of data comparing eastern larch beetle reproductive success, larval development and offspring fitness with environmental temperatures. An understanding of where optimal (or suboptimal) thresholds across these parameters lie in relation to temperature could be used to predict the effects of climate on future population dynamics of eastern larch beetles and the potential for increased forest mortality. Accordingly, a set of laboratory experiments was conducted aiming to: (i) examine how temperature affects the reproductive success of parent beetles; (ii) determine the minimum and optimal temperatures for eastern larch beetle larval development; and (iii) relate the developmental temperature to offspring fitness, using size and lipid content as indicators.

## Materials and methods

### *Source of experimental tamarack material*

Three healthy, non-infested tamaracks with diameter at breast height (1.4 m) of 20.5, 18.9 and 18.6 cm growing in the Red Lake Wildlife Management Area, Lake of the Woods Co., MN, U.S.A. (UTM: 15U 0356131/5387805) were felled and cut to 2-m lengths on 22 October 2011 and transported to the University of Minnesota, St Paul, Minnesota. Log ends were sealed with molten paraffin wax to reduce desiccation and stored at 4 °C until needed.

### *Source of parent eastern larch beetles*

Four tamaracks containing eastern larch beetle brood adults (first larval brood of 2011) were harvested in the Red Lake Wildlife

Management Area (UTM: 15U 0370509/5390453) on 29 October 2011 and brought to the University of Minnesota where the log ends were sealed with molten wax. The logs were stored outdoors throughout the winter of 2011–2012 before being brought into the laboratory and placed in separate emergence tubes at the first sign of beetle emergence on 19 April 2012. Each emergence tube was fitted with a collecting jar for emergent beetles. The infested logs were held at room temperature ( $24 \pm 0.5^\circ\text{C}$ ), at approximately 60% relative humidity, with 24-h ambient light. Emergent beetles were collected daily and separated by date, natal host, and sex. The sex of the beetles was determined using the methods of Lyon (1958). Beetles were stored on moist paper towels at  $4^\circ\text{C}$  and 60% relative humidity until needed.

#### Preparation of material for breeding experiments

Logs from each green tamarack were cut into 20-cm long bolts on 23 April 2012, then split lengthwise into two half-logs (hereafter referred to as 'billets') with standardized bark surface areas of  $360\text{ cm}^2$ , measuring 18 cm in over-the-bark width and 20 cm in length. Molten paraffin wax was used to seal all wood surfaces and bark-wood interfaces to reduce desiccation. Fifty-four billets, 18 from each green tamarack, were prepared and stored at  $4^\circ\text{C}$  for 24 h. The source tamarack for each billet was recorded.

#### Colonization of billets with parent eastern larch beetles and collection of brood adults

On 24 April 2012, the billets were removed from cold storage and allowed to warm to room temperature ( $24^\circ\text{C}$ ) for 24 h. Females were introduced to the billets on 25 April 2012 after being removed from cold storage and allowed 2 h to warm to room temperature. Each billet was colonized with one female–male pair. To introduce a female to a billet, a hole (diameter 5 mm) was drilled through the bark to the surface of the phloem layer. One vigorous female between 3 and 7 days post-emergence and selected at random was then placed in a 0.5-mL, vented Eppendorf tube open at one end. The open end was inserted into the drilled hole such that the female was free to enter the phloem and commence gallery excavation. All females began excavating ovipositional galleries within 4 h of introduction.

Male beetles were introduced to the billets 24 h after the females in the same manner. Most male beetles entered the egg galleries within 30 s. Males were checked after 2 h. Two males that were present in the Eppendorf tubes at this time were replaced with new males that successfully entered the female ovipositional galleries.

Colonized billets were left at room temperature for 24 h to allow the beetle pairs to mate and begin oviposition. This protocol ensured that oviposition commenced at a similar time in all billets, regardless of subsequent rearing temperature treatment. After the 24-h period, each billet was placed in a clear, vented plastic rearing container (width 14 cm, depth 10 cm, length 26 cm) prior to placement in growth chambers under an LD 16 : 8 h photoperiod. Fifty-four pairs of beetles were used (one pair/billet  $\times$  nine billets/rearing temperature  $\times$  six rearing temperatures; see below).

Colonized billets were checked daily for brood emergence beginning 21 days post-colonization. Because parent beetles can re-emerge, the first brood adult was considered to be either the second male or female beetle to emerge, or the third beetle to emerge (i.e. assuming both parent beetles emerged) as described in Smith *et al.* (2009). Upon collection, brood adults were separated by billet, rearing temperature and sex. Collection of brood adults continued until 10 days passed with no new emergence. At this time, the bark was removed from the billets and any remaining, live, non-emergent brood adults were collected to account for all progeny in case some individuals were in a putative diapause state (McKee & Aukema, 2014). Emergent and manually-extracted brood adults were frozen until measured for size and lipid content (see below).

#### Rearing temperature treatments

Studies of beetle development at six rearing temperatures were planned: 10, 14, 18, 22, 26 and  $30^\circ\text{C}$ . During the experiment, repeated malfunctions of the growth chamber for the  $14^\circ\text{C}$  treatment dictated removal of those billets from the experiment. HOBO Data-loggers (Onset Computer Corporation, Bourne, Massachusetts, U.S.A.) in each growth chamber recorded actual rearing temperatures of  $9.9 \pm 0.02$ ,  $19.2 \pm 0.03$ ,  $21.6 \pm 0.005$ ,  $26.1 \pm 0.04$  and  $29.4 \pm 0.016^\circ\text{C}$  (mean  $\pm$  SE) for the intended 10, 18, 22, 26 and  $30^\circ\text{C}$  treatments, respectively. Rearing temperatures recorded by the data loggers were used for all of the analyses.

All billets in the treatments at 19.2, 21.6, 26.1 and  $29.4^\circ\text{C}$  were held at a constant temperature throughout the experiment. The nine billets in the treatment at  $9.9^\circ\text{C}$  were exposed to one of three scenarios as follows. One billet was peeled at day 165 to check whether successful brood development was occurring. These larvae were not used in any analyses. Four of the remaining eight billets were then retained at a constant  $9.9^\circ\text{C}$  for the entire experiment. The remaining four billets were moved from  $9.9^\circ\text{C}$  to the  $19.2^\circ\text{C}$  growth chamber on day 165 to increase chances of successful pupation because temperature thresholds for development were unknown prior to the present study and the mountain pine beetle requires a minimum temperature of  $15^\circ\text{C}$  to successfully pupate (Régnière *et al.*, 2012). The developmental rate of beetles at  $9.9^\circ\text{C}$  ( $\text{RD}_{9.9}$ ) in the temperature-transfer scenario was calculated as:

$$1 = (\text{RD}_{9.9} \times t_{9.9}) + (\text{RD}_{19.2} \times t_{19.2}) \quad (1)$$

where 1 = a constant representing an entire progeny adult as a sum of products of developmental rates (expressed as fractional development of an insect per day) multiplied by the number of days to emergence;  $\text{RD}_{9.9}$  = calculated rate of brood development at  $9.9^\circ\text{C}$  [i.e. 1/time (days) to first emergence];  $t_{9.9} = 165$  = time (days) spent by brood in a billet at  $9.9^\circ\text{C}$ ;  $\text{RD}_{19.2} = 0.0195$  = mean rate of brood development at  $19.2^\circ\text{C}$  [i.e. 1/time (days) to first emergence]; and  $t_{19.2}$  = time (days) spent by brood in a billet at  $19.2^\circ\text{C}$ .

Progeny did complete development at the constant  $9.9^\circ\text{C}$  temperature and so we compared the observed versus the calculated  $\text{RD}_{9.9}$  of beetles reared in constant  $9.9^\circ\text{C}$  and

temperature-transfer 9.9 °C billets, respectively, to validate the calculated  $RD_{9,9}$  values for eastern larch beetles (see Results).

*Measuring the effect of temperature on beetle reproduction, brood development, and brood fitness*

*Brood sex ratio and number of brood per parent female.* All brood adults that emerged or were alive under the bark when the billets were debarked were counted and had the sex determined. All offspring in a billet were the progeny of one female, introduced as part of the single female/male pair to each billet.

*Beetle development time and development rate.* Development time was the number of days from the date of male introduction into a given billet to the date of emergence of the first brood adult from that billet. Beetle development time included the time until the first egg was laid, the time spent as an egg, larva, pupa and teneral adult, and the period of maturation feeding prior to brood adult emergence. Beetle developmental rate was expressed as the inverse of the number of days needed for development.

*Optimal and minimum temperature for brood development.* The optimal temperature for beetle development was calculated using beetle development time in days. A quadratic equation was fit to the number of days needed for beetle development in each billet versus rearing temperature. The minimum point on the line, solved algebraically, corresponded to the optimal developmental temperature defined as the minimum number of days required to complete beetle development.

The minimum developmental temperature was determined using data for development rate plotted against rearing temperatures below the optimal developmental temperature (i.e. 9.9, 19.2, 21.6 and 26.1 °C) where the data formed a linear relationship. After fitting an appropriate statistical model, the equation was solved to determine the temperature where development rate equaled 0.

*Degree days (DD) required for beetle development.* The number of DD required for the development of the first brood adult in each billet at each rearing temperature was calculated using:

$$DD = (t_{\text{mean}} - Dt_{\text{min}}) \times t \quad (2)$$

where  $t_{\text{mean}}$  = mean overall temperature (°C) for the billets in each rearing temperature;  $Dt_{\text{min}} = 7.5$  °C = minimum developmental threshold temperature (°C) of eastern larch beetle (calculated above); and  $t$  = time (days) required for the first brood adult from each billet to develop from an egg to emergent adult.

*Brood adult size and lipid content.* Between 27 and 41 female and male brood adults were subsampled randomly from the each of the 9.9, 19.2, 21.6, 26.1 and 29.4 °C treatments, with the exception of the 9.9 °C temperature-transfer treatment. Progeny size to the nearest 0.01 mm was determined by measuring pronotal width at the widest point using a MZ6 microscope

(Leica Microsystems, Wetzlar, Germany) with real-time camera and digital micrometer. Once measured, insects were dried for 24 h at 50 °C to determine their dry mass (DM). Beetle mass was recorded to the nearest 0.01 mg using an AX105 Delta range analytical microbalance (Mettler-Toledo, Greifensee, Switzerland). Lipids were extracted using a 500-mL Soxhlet extractor with petroleum ether. Dried beetles were placed in individual, screened and labelled 0.5-mL Eppendorf tubes. Sixty-four beetles were processed per lipid extraction using 300 mL of warm petroleum ether. Extractions ran for 8 h with one flush of the extractor column per hour. After extraction, beetles were re-dried for 12 h at 50 °C and re-weighed to the nearest 0.01 mg to obtain the lean dry mass. Total lipid content (mg) per beetle was calculated as the difference in dry mass before and after lipid extraction. Percentage lipid content for each beetle was calculated as a percentage of beetle dry mass prior to lipid extraction (%DM).

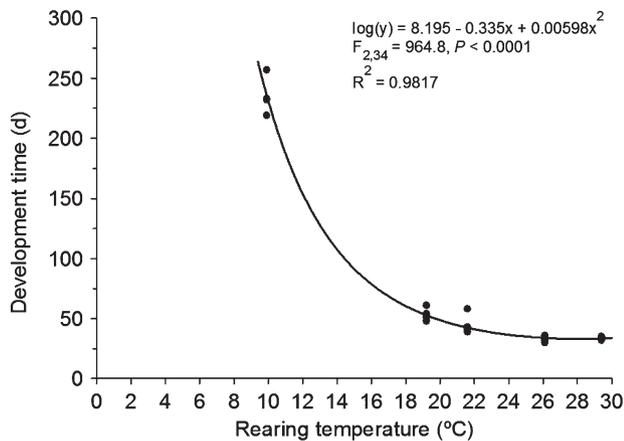
*Statistical analysis*

Analysis of variance (ANOVA) was used to compare observed  $RD_{9,9}$  values of brood from billets in the constant 9.9 °C treatment to the calculated  $RD_{9,9}$  values of brood from billets in the temperature-transfer treatment (9.9 °C moved to 19.2 °C). The effects of rearing temperature on development time, development rate, insect size, mass and lipid content were characterized using separate regression analyses. Variables were transformed as necessary [e.g.  $\text{asin}\sqrt{y}$  for proportional data,  $\log(y + 1)$  or  $\sqrt{y}$  for other variables] to fulfill model assumptions of homoscedasticity and normality of errors. Linear and polynomial models were explored during analyses with final models selected based on model fit (e.g.  $r^2$  values) and simplicity. The number of DD required for brood development versus each rearing temperature was analyzed using ANOVA rather than regression because a lack of fit/pure error test indicated treating rearing temperature as a categorical variable yielded significantly more explanatory power using  $\alpha = 0.05$ . Finally, as a measure of quality control, the effect of host tree was tested for each response variable of interest to detect design artefacts that may have influenced results. The individual tree from which billets originated did not affect any of the variables measured ( $P > 0.05$  for all) and are not treated further. Means separation was conducted using a Tukey's multiple comparisons procedure. All statistical analyses were performed using R (R Development Core Team, 2014).

**Results**

*Number of brood produced per parent female and brood sex ratio.* Offspring production per female averaged  $15.8 \pm 5.1$  progeny across the billets held at a constant 9.9 °C. This production was lower than those billets transferred to a higher temperature ( $40.8 \pm 6.8$  brood adults per female) (ANOVA,  $F_{1,4} = 8.61$ ,  $P = 0.043$ ) and so only the billets held at a constant 9.9 °C were used to compare offspring production across rearing temperatures. Rearing temperature did not affect offspring production ( $F_{2,36} = 1.56$ ,  $P = 0.23$ ). Parent females produced  $44.5 \pm 5.5$  (mean  $\pm$  SE) brood adults overall.

Overall,  $49.2 \pm 2.3\%$  (mean  $\pm$  SE) of the brood adults were females. The brood sex ratio did not differ between billets held

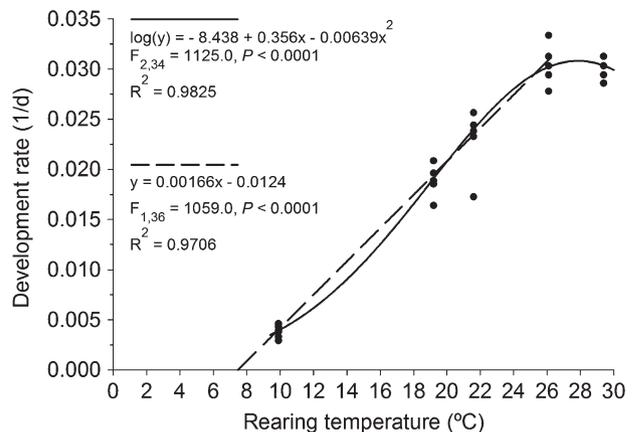


**Figure 1** Number of days needed for eastern larch beetle development from egg to emergent adult at five rearing temperatures. Each point represents the number of days until the emergence of the first brood adult from each billet exposed to a constant rearing temperature. Number of billets = 4, 9, 8, 8, 8 for 9.9, 19.2, 21.6, 26.1 and 29.4 °C temperatures, respectively.

at a constant 9.9 °C and those in the temperature-transfer regime (ANOVA,  $F_{1,4} = 1.059$ ,  $P = 0.36$ ). As such, billets for the constant and temperature-transfer 9.9 °C treatment were pooled. The sex ratio of the offspring was constant across rearing temperatures ( $F_{1,39} = 2.61$ ,  $P = 0.11$ ).

**Beetle development time and optimal developmental temperature.** The number of days needed for brood development decreased with increasing rearing temperature in a curvilinear fashion ( $F_{2,34} = 964.8$ ,  $P < 0.0001$ ) (Fig. 1). The mean  $\pm$  SE number of days required for brood development were  $235.3 \pm 7.9$ ,  $51.6 \pm 1.4$ ,  $43.8 \pm 2.0$ ,  $32.5 \pm 0.7$  and  $33.4 \pm 0.3$  for the constant rearing temperatures of 9.9, 19.2, 21.6, 26.1 and 29.4 °C, respectively. The minimum of this line, from which the optimal developmental temperature was determined, was 27.9 °C. At the optimal temperature, beetles can complete development in 33.2 days.

**Beetle development rate and minimum developmental temperature.** The observed  $RD_{9.9}$  for beetles in billets held at a constant 9.9 °C were not different from the calculated  $RD_{9.9}$  for beetles in the 9.9 °C temperature-transfer billets ( $F_{1,4} = 2.52$ ,  $P = 0.19$ ) and so the  $RD_{9.9}$  data were pooled for further analyses. The mean  $\pm$  SE  $RD_{9.9}$  values were  $0.0043 \pm 0.00014$  and  $0.0037 \pm 0.00037$  for the 9.9 °C constant and temperature-transfer billets, respectively. The rate of beetle development [i.e. (1/development time (days))] increased with increasing rearing temperature ( $F_{2,38} = 1125.0$ ,  $P < 0.0001$ ) (Fig. 2, solid line). Mean  $\pm$  SE developmental rates were  $0.00396 \pm 0.000217$ ,  $0.0195 \pm 0.000501$ ,  $0.0232 \pm 0.000838$ ,  $0.0309 \pm 0.000660$  and  $0.0299 \pm 0.000274$  for rearing temperatures of 9.9, 19.2, 21.6, 26.1 and 29.4 °C, respectively. Data from the linear portion of the developmental rate curve (i.e. 9.9, 19.2, 21.6 and 26.1 °C) were used to calculate the minimum developmental threshold of 7.5 °C (Fig. 2, dashed line).

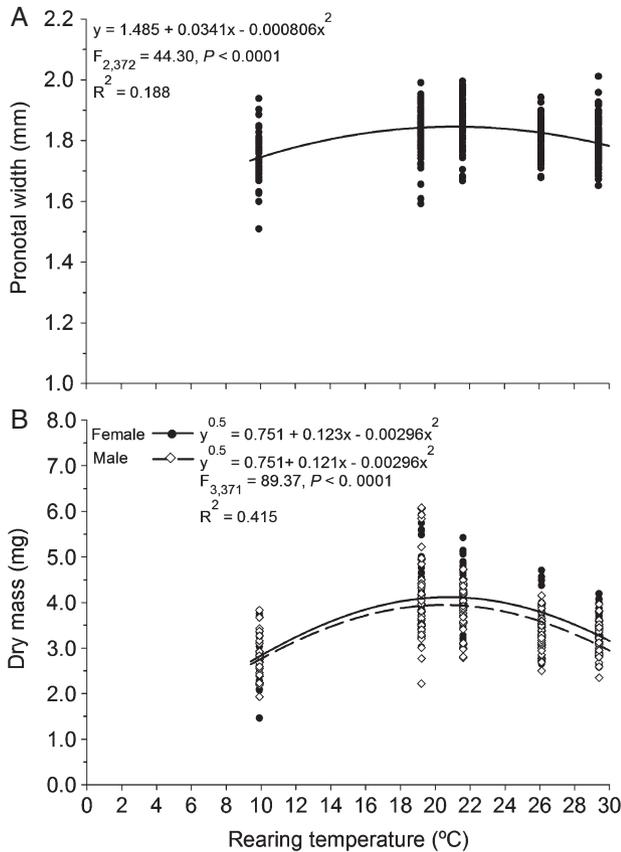


**Figure 2** Developmental rates of eastern larch beetles at five rearing temperatures. Each point represents the developmental rate of the first brood adult to emerge from each billet. Number of billets = 8, 9, 8, 8, 8 for 9.9, 19.2, 21.6, 26.1 and 29.4 °C temperatures, respectively.

**The effect of rearing temperature on offspring size and dry mass.** The pronotal widths of female and male brood adults were  $1.82 \pm 0.0059$  and  $1.81 \pm 0.0060$  mm, respectively. Because this difference was not statistically significant (ANOVA,  $F_{1,371} = 0.65$ ,  $P = 0.42$ ) and no interaction existed between beetle sex and rearing temperature on beetle size (ANOVA,  $F_{1,371} = 0.25$ ,  $P = 0.62$ ), data for female and male beetles were pooled. The largest brood adults occurred at 21.1 °C, with progeny becoming slightly smaller at both cooler and warmer temperatures ( $F_{2,372} = 44.3$ ,  $P < 0.0001$ ) (Fig. 3A). Even though males and females were similar in size, the females exhibited greater mean  $\pm$  SE dry mass than male brood adults ( $3.67 \pm 0.056$  versus  $3.49 \pm 0.052$  mg, respectively; ANOVA,  $F_{1,373} = 5.65$ ,  $P = 0.018$ ). There was an interaction between beetle sex and rearing temperature on beetle dry mass (ANOVA,  $F_{1,371} = 11.78$ ,  $P < 0.001$ ). The heaviest female and male brood adults were produced at 20.8 and 20.4 °C, respectively, with lighter progeny developing both above and below these temperatures (Fig. 3B).

**The effect of beetle dry mass on total and percentage lipid content.** Beetle total lipid content (mg) was positively correlated with beetle dry mass (mg) ( $r^2 = 0.790$ ) (ANOVA,  $F_{1,373} = 1410.7$ ,  $P < 0.0001$ ) (Fig. 4A). This relationship was consistent between males and females (ANOVA,  $F_{1,372} = 0.46$ ,  $P = 0.50$ ) and so beetles were pooled. Beetle percentage lipid content (%DM) had a positive curvilinear relationship with beetle dry mass (mg) ( $r^2 = 0.531$ ) (ANOVA,  $F_{2,372} = 212.5$ ,  $P < 0.0001$ ) (Fig. 4B). Percentage lipid content was not affected by beetle sex (ANOVA,  $F_{1,370} = 0.23$ ,  $P = 0.63$ ) or by an interaction between beetle sex and dry mass (ANOVA,  $F_{1,370} = 0.28$ ,  $P = 0.60$ ) and so data for both sexes were pooled.

**The effect of rearing temperature on the total and percentage lipid content of offspring.** The total lipid (mg) content of female brood adults was significantly greater than that of males, averaging  $0.92 \pm 0.032$  and  $0.81 \pm 0.030$  mg, respectively (ANOVA,  $F_{1,373} = 5.89$ ,  $P = 0.016$ ). Total lipid content had a concave



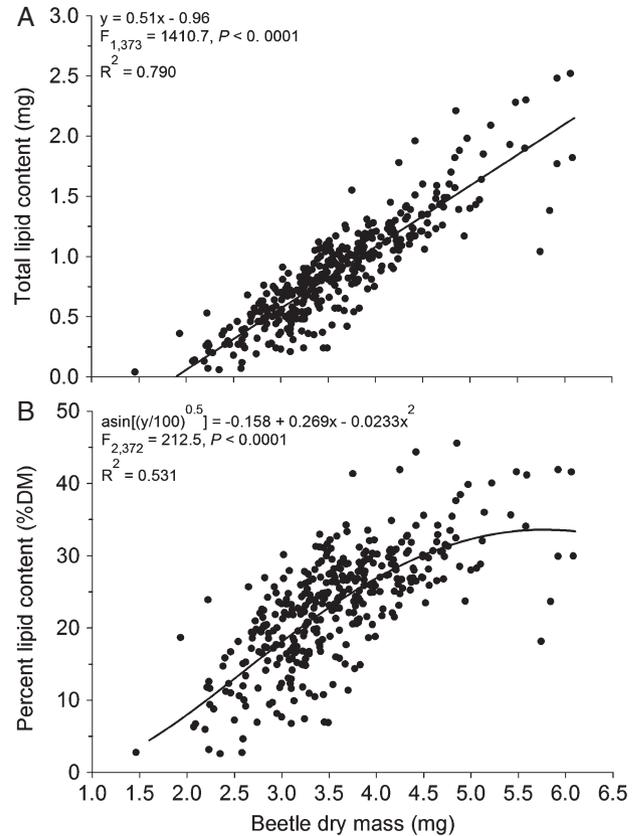
**Figure 3** (A) Pronotal width (mm) of eastern larch beetle brood adults at five rearing temperatures. (B) Dry mass (mg) of eastern larch beetle brood adults at five rearing temperatures. For each graph, each point represents one beetle ( $n = 186$  females,  $189$  males). Male and female beetles were pooled when considered appropriate by statistical analyses.

parabolic relationship with rearing temperature ( $F_{2,371} = 272.9$ ,  $P < 0.0001$ ) that was influenced by beetle sex ( $F_{1,371} = 10.0$ ,  $P < 0.0001$ ). Progeny had the greatest total lipid content at temperatures of  $20.2^\circ\text{C}$  for females and  $19.7^\circ\text{C}$  for males (Fig. 5A).

Percentage lipid content (%DM) of brood adults averaged  $23.9 \pm 0.6$  and  $22.3 \pm 0.5\%$  overall for female and male beetles, respectively, and did not differ significantly (ANOVA,  $F_{1,373} = 3.27$ ,  $P = 0.07$ ). Beetles were pooled by sex for further analyses. The optimum rearing temperature for percentage lipid content of brood adults was  $20.2^\circ\text{C}$ , where insects exhibited  $27.9\%$  lipid content on average. There was substantial variability in this relationship, however, with only  $38.7\%$  of the variation in the data explained by the regression line ( $F_{2,372} = 119.0$ ,  $P < 0.0001$ ) (Fig. 5B).

#### Number of DD needed for eastern larch beetle development.

The mean  $\pm$  SE number of DD  $\geq 7.5^\circ\text{C}$  required for a beetle to develop from an egg to an emergent brood adult did not differ among rearing temperatures below the optimal developmental temperature of  $27.9^\circ\text{C}$  but was significantly greater for the  $29.4^\circ\text{C}$  rearing temperature (ANOVA,  $F_{4,32} = 10.1$ ,  $P < 0.001$ ) (Fig. 6). The mean  $\pm$  SE DD requirements for brood development from egg to progeny emergence were  $604.1 \pm 9.1$  when pooled



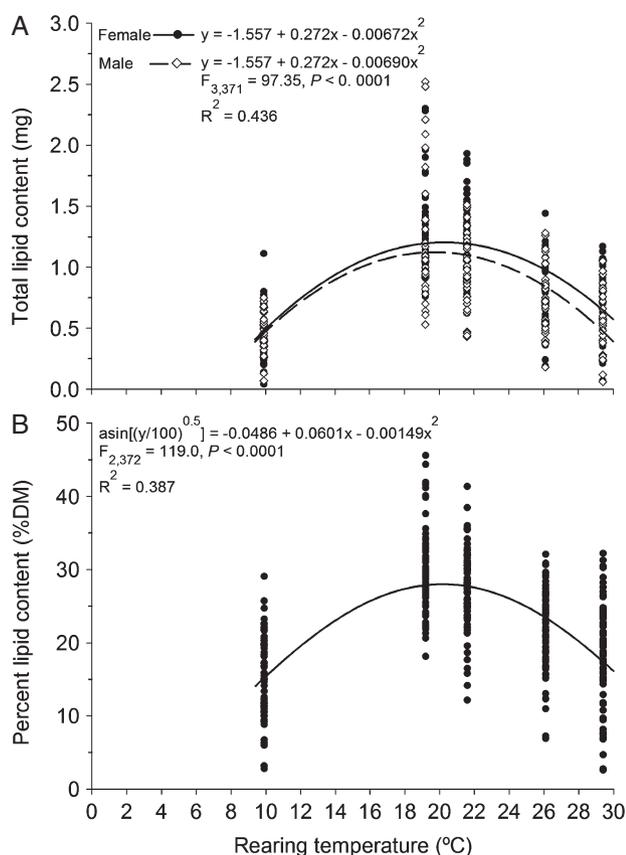
**Figure 4** The effect of beetle dry mass (mg) on (A) total lipid content (mg) and (B) percentage lipid content (%DM) of eastern larch beetle brood adults. Beetles from all rearing temperatures were pooled. Each point represents one beetle ( $n = 186$  females,  $189$  males).

for rearing temperatures below  $27.9^\circ\text{C}$ . At  $29.4^\circ\text{C}$ ,  $732.3 \pm 6.7$  DD were required for development.

## Discussion

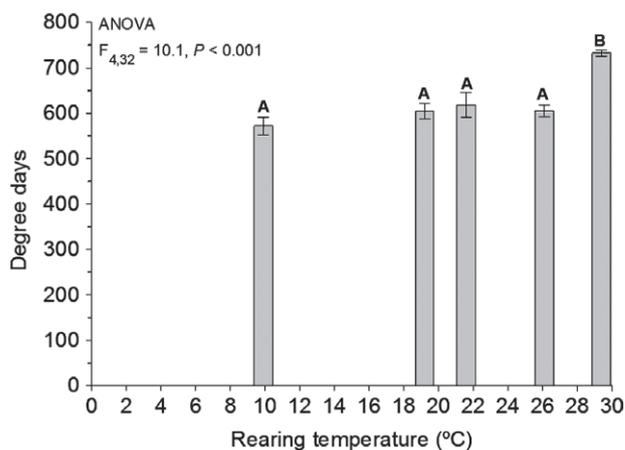
Successful progeny development and emergence at a constant  $9.9^\circ\text{C}$  demonstrates that the minimum developmental thresholds of all life stages of the eastern larch beetle are  $\leq 9.9^\circ\text{C}$  or that the subadult life stages lack individualized minimum developmental thresholds. The spruce beetle, similar to the eastern larch beetle, can also complete development at temperatures below  $10^\circ\text{C}$  but is subject to a facultative larval diapause that results in a semi- versus univoltine lifecycle (Hansen *et al.*, 2001, 2011). Inclusion of a treatment at  $14^\circ\text{C}$  may have allowed us to detect a similar larval or prepupal diapause, although reports of a univoltine lifecycle for eastern larch beetles from cool, northern latitudes (Werner, 1986) suggest that this insect lacks any subadult diapause.

Other than diapause, prevention of development to cold-sensitive life stages such as pupae and adults can also be achieved through higher developmental temperature thresholds of larval life stages. In mountain pine beetle, for example, developmental thresholds of late-instar larvae and pupae of  $16.2$  and  $15^\circ\text{C}$ , respectively, slow development as autumn



**Figure 5** (A) Total lipid content (mg) and (B) percentage lipid content (%DM) of eastern larch beetle brood adults at five rearing temperatures. Each point represents one beetle ( $n = 186$  females, 189 males). Male and female beetles were pooled as deemed appropriate by statistical analyses.

temperatures decline and so pupae and adults are not typically subjected to lethal winter temperatures (Bentz *et al.*, 1991; Régnière *et al.*, 2012). The selective pressure to evolve high developmental thresholds at subadult life stages may be reduced for eastern larch beetles, however, because adults are quite cold hardy (Venette & Walter, 2008). Indeed, beetles colonize hosts early in the spring such that larval development to the cold-hardy adult life stages is largely complete prior to onset of freezing winter temperatures. Moreover, the behaviour of many brood adults to migrate from pupal chambers to the tree base to over-winter beneath the snow line also reduces winter mortality (Hopkins, 1909; Simpson, 1929; Werner, 1986; Langor & Raske, 1987a). Developmental thresholds, such as those for fourth-instar development and for pupation in the mountain pine beetle (Régnière *et al.*, 2012), also act to synchronize beetle emergence and host procurement activities to the summer months when water deficit conditions enhance tree vulnerability to beetle attack (Logan & Bentz, 1999; Powell & Logan, 2005; Safranyik & Carroll, 2006; Régnière *et al.*, 2012). By contrast, eastern larch beetle adults attack host trees early in the spring when translocation of oleoresin may be reduced by frozen root systems for tamaracks growing in cold climates or in areas with saturated soils (Werner, 1986; F.R. McKee,



**Figure 6** Number of degree days  $\geq 7.5$  °C needed for eastern larch beetles to develop from eggs to emergent brood adults at five rearing temperatures of 9.9, 19.2, 21.6, 26.1 and 29.4 °C. Degree days were recorded for the first brood adult to emerge from each infested tamarack billet at each rearing temperature. Number of billets = 4, 9, 8, 8, 8 for 9.9, 19.2, 21.6, 26.1 and 29.4 °C temperatures, respectively.

personal observation). Developmental thresholds pose major constraints to bivoltine development in mountain pine beetles (Bentz *et al.*, 2014). However, reduced physiological limitations to development at low temperatures (i.e.  $\leq 9.9$  °C) as a result of low developmental thresholds for the life stages of eastern larch beetles may allow this insect to shift voltinism in response to climate warming quite readily.

Although previous studies indicate a diapause for eastern larch beetle adults (Swaine, 1911; Simpson, 1929; Langor & Raske, 1987b), recent laboratory (McKee & Aukema, 2014) and field studies (F. R. McKee & B. H. Aukema, unpublished data) suggest that an adult diapause is facultative. Moreover, the high optimal developmental temperature of 27.9 °C for eastern larch beetles suggests that eastern larch beetles could take advantage of additional heat units as a result of climate change without developmental complications. Indeed, the maximum developmental rate, averaged across all life stages, occurs at a higher temperature for eastern larch beetles than for the mountain pine beetle (25 °C) and is within the range reported for southern pine beetle (27–30 °C) (Wagner *et al.*, 1983; Stephen, 2011; Régnière *et al.*, 2012). Some bark beetle species with large geographical ranges exhibit regional adaptations to prevailing climatic conditions that alter the effect of temperature on beetle development, such that populations from northern latitudes develop faster at a given constant temperature (Bentz *et al.*, 2001, 2011; Bracewell *et al.*, 2013). Similar relationships also likely exist in eastern larch beetles because populations from higher latitudes in the Canadian Maritimes take 80, 42 and 40 days to develop at 12, 18 and 24 °C, respectively (Langor & Raske, 1987b), whereas the data in the present study indicate developmental times of 154, 61 and 37 days for the same temperatures for populations representing the near-southern extent of the eastern larch beetle distribution (Fig. 1) (Seybold *et al.*, 2002). If eastern larch beetles from higher latitudes possess the ability to develop faster than the beetles observed in the present study when exposed to similar environmental

temperatures, this system may be highly sensitive to climate warming on a broad scale. As is the case with the mountain pine beetle (Bentz *et al.*, 2001, 2011), adaptation of eastern larch beetle populations to local climate is likely to synchronize beetle activity at the landscape scale. Under climate warming scenarios, the sensitivity of eastern larch beetle development to temperature may become manifested as an increase in the number of larval broods that are established and that successfully develop to adults each year. An increase in the number of eastern larch beetle larval broods produced each year may result in an increased frequency and severity of beetle outbreaks and tamarack mortality.

Our method of using infested billets (Smith *et al.*, 2009) rather than phloem sandwiches (Hansen *et al.*, 2011) yields a developmental rate averaged across all life stages, rather than rates specific to each life stage, which vary among the eastern larch beetle (Langor & Raske, 1987b) and several other species of bark beetles (Vité & Rudinsky, 1957; Bentz *et al.*, 1991; Wermelinger & Seifert, 1998; Hansen *et al.*, 2001). In the present study, we are most interested in minimum and optimal thresholds for complete development, and do not capture variability across all progeny. Later-emerging progeny at a given temperature, for example, could reflect a later date of oviposition or a reduced development rate, or both. We also note that linear extrapolation of development rate data to estimate the minimum temperature for development may over-estimate the lower developmental threshold (Beck, 1983; Wermelinger & Seifert, 1998; Briere *et al.*, 1999), although the difference of 20.4 °C between our estimates of optimal (27.9 °C) and minimum (7.5 °C) developmental temperatures falls within the related 95% confidence interval of 19.1–20.5 °C reported by Dixon *et al.* (2009) for most temperate insects. The lower developmental threshold temperature for eastern larch beetles calculated in the present study is quite similar to that reported for its closest relative, the Douglas-fir beetle *Dendroctonus pseudotsugae* Hopkins of approximately 8 °C (Vité & Rudinsky, 1957).

Bias in the sex ratios of eastern larch beetles are reported for field populations (Werner, 1986; Langor & Raske, 1987b), although this was not present in the beetles of our laboratory study, suggesting that rearing temperatures between 10 and 30 °C were not sufficient to induce unequal survivorship between sexes. Brood sex ratios in bark beetles can become skewed to favour the fittest sex in the presence of some stressing agent (Amman & Pace, 1976), such as competition, predation and/or parasitism, host defences, desiccation, or lethal overwintering temperatures affecting juvenile life stages (Cole, 1973; Amman, 1984; Rankin & Borden, 1991). In some bark beetles, sex ratios favour the host selecting sex (Bentz *et al.*, 2011; Lachowsky & Reid, 2014), although this is inconsistent (Safranyik & Whitney, 1985; Wermelinger & Seifert, 1999; Bentz *et al.*, 2014). Although little is known regarding beetle mortality between host emergence and procurement (Raffa, 2001), host-seeking behaviour in this system may skew sex ratios if females with greater lipid content than males are better conditioned dispersers (Evenden *et al.*, 2014).

Although the host selecting sex in scolytid beetles is usually larger (Wood, 1982), we did not find this to be the case in the present study, mirroring inconsistencies among field-captured populations of eastern larch beetles (Werner, 1986; Langor &

Raske, 1987b). Moreover, we did not find that cooler temperatures resulted in larger offspring as has been reported in other bark beetles (Atkins, 1967; Safranyik & Whitney, 1985; Bentz *et al.*, 2001) and insects in general (Roff, 1980; Nylin & Gotthard, 1998; Kingsolver & Huey, 2008). In the present study, the largest offspring were produced between 21 and 22 °C (Fig. 3). A similar relationship has also been observed in the pine weevil *Hylobius abietis* (Inward *et al.*, 2012). Smaller progeny at the lower and upper rearing temperatures may be a result of temperature stress (Kingsolver & Huey, 2008). Larger body sizes are often associated with greater survival, fecundity, mating success and dispersal potential (McGhehey, 1971; Roff, 1980; Anderbrant, 1988; Honěk, 1993; Kingsolver & Huey, 2008; Williams & Robertson, 2008; Evenden *et al.*, 2014). Similar to body size–temperature relationships, the peak in lipid content for beetles that developed at temperatures of approximately 20 °C suggests that these beetles possess a fitness advantage relative to beetles that develop at other temperatures because increased lipid content, similar to larger body size, has also been shown to increase dispersal, survival, host attack and fecundity in bark beetles (Atkins, 1966; Thompson & Bennett, 1971; Anderbrant, 1988; Jactel, 1993; Elkin & Reid, 2005; Williams & Robertson, 2008; Evenden *et al.*, 2014). The optimal temperature for developmental rate, however, occurred at a much higher temperature of 27.9 °C. This incongruence of optimal temperatures for size, lipid content and development rate may represent confounding developmental effects of associated symbionts, such as fungi (Jacobs *et al.*, 1997), which provide nourishment to developing beetles (Bentz & Six, 2006; Bleiker & Six, 2007).

This potential trade-off between developmental rate, beetle size and beetle lipid content may help to maximize beetle survival and reproductive potential over a wide range of temperatures and environmental conditions. For example, warmer temperatures may not only foster higher rates of insect development and increased potential for population growth, but also result in smaller, less lipid-rich offspring (Nylin & Gotthard, 1998). Bark beetles must attack host trees in sufficient numbers to kill part, or all of, the host tree to overcome host defences and reproduce successfully (Raffa & Berryman, 1987; Raffa *et al.*, 2005). Thus, when conditions are sub-optimal for development (i.e. cool temperatures) and beetle population growth potential is low, larger and more lipid-rich individuals may increase individual survivorship when fewer beetles are available to participate in host attack and the risk of mortality for each individual is greater (Raffa & Berryman, 1983, 1987). Conversely, warm environmental conditions that promote rapid beetle development may also result in smaller, less lipid-rich individuals that experience reduced survivorship when attacking host trees individually. However, the advantage offered by a larger population of beetles to cooperatively attack a host tree helps to ensure successful host tree colonization and beetle reproduction and also allows the beetle population to increase.

Several aspects of the biology of the eastern larch beetle related to temperature, such as the absence of an obligate diapause, a high optimal developmental temperature and a minimal developmental temperature for all life stages below 9.9 °C, suggest that this insect has the potential to become problematic under climate change scenarios and cause more forest mortality than previously observed. This would be especially true if this insect

could become bivoltine because patterns of voltinism in forest insects have enormous ramifications for the potential of an insect to undergo population outbreaks and cause significant forest mortality. We are currently examining temperature signals at landscape levels to determine whether implications for population increase from our laboratory study are realized by changes in forest mortality in the field.

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## References

- Albers, M.A. (2010) *Eastern Larch Beetle in Minnesota*. Minnesota Department of Natural Resources, Forest Health Unit, Grand Rapids, Minnesota.
- Alfaro, R.I., Campbell, E. & Hawkes, B.C. (2010) *Historical Frequency, Intensity and Extent of Mountain Pine Beetle Disturbance in British Columbia*. Mountain Pine Beetle Working Paper 2009–30. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Canada.
- Amman, G.D. (1984) Mountain pine beetle (Coleoptera: Scolytidae) mortality in three types of infestations. *Environmental Entomology*, **13**, 184–191.
- Amman, G.D. & Pace, V.E. (1976) *Optimum Egg Gallery Densities for the Mountain Pine Beetle in Relation to Lodgepole Pine Phloem Thickness*. Research Note INT-209. United States Department of Agriculture – Forest Service, Intermountain Forest & Range Experiment Station, Ogden, Utah.
- Anderbrant, O. (1988) Survival of parent and brood adult bark beetles, *Ips typographus*, in relation to size, lipid content and re-emergence or emergence day. *Physiological Entomology*, **13**, 121–129.
- Atkins, M.D. (1966) Laboratory studies on the behaviour of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins. *Canadian Entomologist*, **98**, 953–991.
- Atkins, M.D. (1967) The effect of rearing temperature on the size and fat content of the Douglas-fir beetle. *Canadian Entomologist*, **99**, 181–187.
- Aukema, B.H., Carroll, A.L., Zhu, J., Raffa, K.F., Sickley, T.A. & Taylor, S.W. (2006) Landscape level analysis of mountain pine beetle in British Columbia, Canada: spatiotemporal development and spatial synchrony within the present outbreak. *Ecography*, **29**, 427–441.
- Aukema, B.H., Carroll, A.L., Zheng, Y. *et al.* (2008) Movement of outbreak populations of mountain pine beetle: influences of spatiotemporal patterns and climate. *Ecography*, **31**, 348–358.
- Bale, J.S., Masters, G.J., Hodkinson, I.D. *et al.* (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology*, **8**, 1–16.
- Beck, S.D. (1983) Insect thermoperiodism. *Annual Review of Entomology*, **28**, 91–108.
- Bentz, B.J. & Six, D.L. (2006) Ergosterol content of fungi associated with *Dendroctonus ponderosae* and *Dendroctonus rufipennis* (Coleoptera: Curculionidae, Scolytinae). *Annals of the Entomological Society of America*, **99**, 189–194.
- Bentz, B.J., Logan, J.A. & Amman, G.D. (1991) Temperature-dependent development of the mountain pine beetle (Coleoptera: Scolytidae) and simulation of its phenology. *Canadian Entomologist*, **123**, 1083–1094.
- Bentz, B.J., Logan, J.A. & Vandygriff, J.C. (2001) Latitudinal variation in *Dendroctonus ponderosae* (Coleoptera: Scolytidae) development time and adult size. *Canadian Entomologist*, **133**, 375–387.
- Bentz, B.J., Régnière, J., Fettig, C.J. *et al.* (2010) Climate change and bark beetles of the western United States and Canada: direct and indirect effects. *BioScience*, **60**, 602–613.
- Bentz, B.J., Bracewell, R.R., Mock, K.E. & Pfrender, M.E. (2011) Genetic architecture and phenotypic plasticity of thermally-regulated traits in an eruptive species, *Dendroctonus ponderosae*. *Evolutionary Ecology*, **25**, 1269–1288.
- Bentz, B.J., Vandygriff, J.C., Jensen, C. *et al.* (2014) Mountain pine beetle voltinism and life history characteristics across latitudinal and elevational gradients in the western United States. *Forest Science*, **60**, 1–16.
- Berg, E.E., Henry, J.D., Fastie, C.L., De Volder, A.D. & Matsuoka, S.M. (2006) Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Klauane National Park and Reserve, Yukon Territory: relationship to summer temperatures and regional differences in disturbance regimes. *Forest Ecology and Management*, **227**, 219–232.
- Bleiker, K.P. & Six, D.L. (2007) Dietary benefits of fungal associates to an eruptive herbivore: potential implications of multiple associates on host population dynamics. *Environmental Entomology*, **36**, 1384–1396.
- Bracewell, R.R., Pfrender, M.E., Mock, K.E. & Bentz, B.J. (2013) Contrasting geographic patterns of genetic differentiation in body size and development time with reproductive isolation in *Dendroctonus ponderosae* (Coleoptera: Curculionidae, Scolytinae). *Annals of the Entomological Society of America*, **106**, 385–391.
- Briere, J.-F., Pracros, P., Le Roux, A.-Y. & Pierre, J.-S. (1999) A novel rate model of temperature-dependent development for arthropods. *Environmental Entomology*, **28**, 22–29.
- Burns, R.M. & Honkala, B.H. (1990) *Silvics of North America: 1. Conifers; 2. Hardwoods*, Vol. 2, Agriculture Handbook 654. United States Department of Agriculture – Forest Service, Washington, District of Columbia.
- Carroll, A.L., Taylor, S.W., Régnière, J. & Safranyik, L. (2004) Effects of climate change on range expansion by the mountain pine beetle in British Columbia. Mountain Pine Beetle Symposium: Challenges and Solutions, 30–31 October 2003, Kelowna, British Columbia (ed. by T. L. Shore, J. E. Brooks and J. E. Stone), pp. 223–232. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Canada.
- Chapman, T.B., Veblen, T.T. & Schoennagel, T. (2012) Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. *Ecology*, **93**, 2175–2185.
- Cole, W.E. (1973) Crowding effects among single-age larvae of the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae). *Environmental Entomology*, **2**, 285–293.
- Dixon, A.F.G., Honěk, A., Keil, P., Kotela, M.A.A., Šizling, A.L. & Jarošík, V. (2009) Relationship between the minimum and maximum temperature thresholds for development in insects. *Functional Ecology*, **23**, 257–264.
- Elkin, C.M. & Reid, M.L. (2005) Low energy reserves and energy allocation decisions affect reproduction by mountain pine beetles, *Dendroctonus ponderosae*. *Functional Ecology*, **19**, 102–109.

- Evenden, M.L., Whitehouse, C.M. & Sykes, J. (2014) Factors influencing flight capacity of the mountain pine beetle (Coleoptera: Curculionidae: Scolytinae). *Environmental Entomology*, **43**, 187–196.
- Hansen, E.M., Bentz, B.J. & Turner, D.L. (2001) Physiological basis for flexible voltinism in the spruce beetle (Coleoptera: Scolytidae). *Canadian Entomologist*, **133**, 805–817.
- Hansen, E.M., Bentz, B.J., Powell, J.S., Gray, D.R. & Vandygriff, J.C. (2011) Prepupal diapause and instar IV developmental rates of the spruce beetle, *Dendroctonus rufipennis* (Coleoptera: Curculionidae, Scolytinae). *Journal of Insect Physiology*, **57**, 1347–1357.
- Hart, S.J., Veblen, T.T., Eisenhart, K.S., Jarvis, D. & Kulakowski, D. (2014) Drought induces spruce beetle (*Dendroctonus rufipennis*) outbreaks across northwestern Colorado. *Ecology*, **95**, 930–939.
- Hicke, J.A., Allen, C.D., Desai, A.R. *et al.* (2012) Effects of biotic disturbances on forest carbon cycling in the United States and Canada. *Global Change Biology*, **18**, 7–34.
- Holsten, E.H., Thier, R.W., Munson, A.S. & Gibson, K.E. (1999) *The Spruce Beetle*. Forest Insect & Disease Leaflet #127. USDA – Forest Service, Washington, District of Columbia.
- Honěk, A. (1993) Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos*, **66**, 483–492.
- Hopkins, A.D. (1909) *The Eastern Larch Beetle. The Douglas Fir Beetle*. Bulletin #83, Part #1. USDA – Bureau of Entomology, Washington, District of Columbia.
- Inward, D.J.G., Wainhouse, D. & Peace, A. (2012) The effect of temperature on the development and life cycle regulation of the pine weevil *Hyllobius abietis* and the potential impacts of climate change. *Agricultural and Forest Entomology*, **14**, 348–357.
- Jacobs, K., Wingfield, M.J. & Bergdahl, D.R. (1997) A new *Ophiostoma* species with a *Graphium* anamorph from *Larix laricina* in eastern North America. *Mycologia*, **89**, 332–338.
- Jactel, H. (1993) Individual variability in the flight potential of *Ips sexdentatus* Boern. (Coleoptera: Scolytidae) in relation to day of emergence, sex, size, and lipid content. *Canadian Entomologist*, **125**, 919–930.
- Jenkins, M.J., Hebertson, E.G. & Munson, A.S. (2014) Spruce beetle biology, ecology and management in the Rocky Mountains: an addendum to spruce beetle in the Rockies. *Forests*, **5**, 21–71.
- Kingsolver, J.G. & Huey, R.B. (2008) Size, temperature, and fitness: three rules. *Evolutionary Ecology Research*, **10**, 251–268.
- Kurz, W.A., Dymond, C.C., Stinson, G. *et al.* (2008) Mountain pine beetle and forest carbon feedback to climate change. *Nature*, **452**, 987–990.
- Lachowsky, L.E. & Reid, M.L. (2014) Developmental mortality increases sex-ratio bias of a size-dimorphic bark beetle. *Ecological Entomology*, **39**, 300–308.
- Langor, D.W. & Raske, A.G. (1987a) Emergence, host attack, and overwintering behavior of the eastern larch beetle, *Dendroctonus simplex* LeConte (Coleoptera: Scolytidae), in Newfoundland. *Canadian Entomologist*, **119**, 975–983.
- Langor, D.W. & Raske, A.G. (1987b) Reproduction and development of the eastern larch beetle, *Dendroctonus simplex* LeConte (Coleoptera: Scolytidae), in Newfoundland. *Canadian Entomologist*, **119**, 985–992.
- Langor, D.W. & Raske, A.G. (1989a) The eastern larch beetle, another threat to our forests (Coleoptera: Scolytidae). *Forestry Chronicle*, **65**, 276–279.
- Langor, D.W. & Raske, A.G. (1989b) A history of the eastern larch beetle, *Dendroctonus simplex* (Coleoptera: Scolytidae), in North America. *Great Lakes Entomologist*, **22**, 139–154.
- Logan, J.A. & Bentz, B.J. (1999) Model analysis of mountain pine beetle (Coleoptera: Scolytidae) seasonality. *Environmental Entomology*, **28**, 924–934.
- Lyon, R.L. (1958) A useful secondary sex character in *Dendroctonus* bark beetles. *Canadian Entomologist*, **90**, 582–584.
- MBCFB, Manitoba Conservation Forestry Branch (2014) *Eastern Larch Beetle Outbreak in Manitoba*. [online] [WWW document]. URL <https://www.gov.mb.ca/conservation/forestry/health/eastern-larch.html> [accessed on 18 March 2014].
- McGhehey, J.H. (1971) *Female Size and Egg Production of the Mountain Pine Beetle*, *Dendroctonus ponderosae* Hopkins. Information Report No NOR-X-9. Northern Forest Research Centre, Canadian Forestry Service, Department of the Environment, Canada.
- McKee, F.R. & Aukema, B.H. (2014) Successful reproduction by the eastern larch beetle (*Dendroctonus simplex*) in the absence of an over-wintering period. *Canadian Entomologist*, in press.
- MIDNR, Michigan Department of Natural Resources (2013) *2013 Forest Health Highlights*. Michigan Department of Natural Resources, Lansing, Michigan.
- MNDNR, Minnesota Department of Natural Resources (2012) *Minnesota Forest Health 2012 Annual Report*. Minnesota Department of Natural Resources – Forestry, Forest Health Unit, St Paul, Minnesota.
- MNDNR, Minnesota Department of Natural Resources (2013) *2013 Minnesota Pest Conditions Report*. Minnesota Department of Natural Resources – Forestry, Forest Health Unit, St Paul, Minnesota.
- Nylin, S. & Gotthard, K. (1998) Plasticity in life-history traits. *Annual Review of Entomology*, **43**, 63–83.
- ONMNR, Ontario Ministry of Natural Resources (2012) *Forest Health Conditions in Ontario, 2011* (ed. by T. A. Scarr, K. L. Ryall and P. Hodge), p. 57. Ontario Ministry of Natural Resources, Canada.
- Powell, J.A. & Logan, J.A. (2005) Insect seasonality: circle map analysis of temperature-driven life cycles. *Theoretical Population Biology*, **67**, 161–179.
- Prendergast, B.F. (1991) *The chemical ecology of the eastern larch beetle, Dendroctonus simplex* LeConte, and the spruce beetle, *D. rufipennis* (Kirby). MSc Thesis, State University of New York.
- Raffa, K.F. (2001) Mixed messages across multiple trophic levels: the ecology of bark beetle chemical communication systems. *Chemoecology*, **11**, 49–65.
- Raffa, K.F. & Berryman, A.A. (1983) The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). *Ecological Monographs*, **53**, 27–49.
- Raffa, K.F. & Berryman, A.A. (1987) Interacting selective pressures in conifer–bark beetle systems: a basis for reciprocal adaptations? *American Naturalist*, **129**, 234–262.
- Raffa, K.F., Aukema, B.H., Erbilgin, N., Klepzig, K.D. & Wallin, K.F. (2005) Interactions among conifer terpenoids and bark beetles across multiple levels of scale: an attempt to understand links between population patterns and physiological processes. *Recent Advances in Phytochemistry*, **39**, 79–118.
- Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G. & Romme, W.H. (2008) Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioScience*, **58**, 501–517.
- Rankin, L.J. & Borden, J.H. (1991) Competitive interactions between the mountain pine beetle and the pine engraver in lodgepole pine. *Canadian Journal of Forest Research*, **21**, 1029–1036.
- R Development Core Team (2014) The R Project for Statistical Computing [WWW document]. URL <http://www.r-project.org/> [accessed 25 August 2012].
- Régnière, J., Powell, J.A., Bentz, B.J. & Nealis, V.G. (2012) Effects of temperature on development, survival and reproduction of insects: experimental design, data analysis and modeling. *Journal of Insect Physiology*, **58**, 634–647.
- Roff, D. (1980) Optimizing development time in a seasonal environment: the ‘ups and downs’ of clinal variation. *Oecologia*, **45**, 202–208.
- Safranyik, L. & Carroll, A.L. (2006) The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. *The Mountain Pine Beetle: A Synthesis of Biology, Management, and Impacts on*

- Lodgepole Pine* (ed. by L. Safranyik and B. Wilson), pp. 3–66. Natural Resources Canada, Pacific Forestry Centre, Canada.
- Safranyik, L. & Whitney, H.S. (1985) Development and survival of mountain pine beetles, *Dendroctonus ponderosae* (Coleoptera: Scolytidae), reared at constant temperatures. *Canadian Entomologist*, **117**, 185–192.
- Sambaraju, K.R., Carroll, A.L., Zhu, J., Stahl, K., Moore, R.D. & Aukema, B.H. (2011) Climate change could alter the distribution of mountain pine beetle outbreaks in western Canada. *Ecography*, **34**, 001–013.
- Seybold, S.J., Albers, M.A. & Katovich, S.A. (2002) *Eastern Larch Beetle*. Forest Insect & Disease Leaflet #175. US Department of Agriculture – Forest Service, Northern Research Station, St Paul, Minnesota.
- Simpson, L.J. (1929) The biology of Canadian bark beetles. The seasonal history of *Dendroctonus simplex* LeC. *Canadian Entomologist*, **61**, 274–279.
- Smith, G.D., Carroll, A.L. & Lindgren, B.S. (2009) Life history of a secondary bark beetle, *Pseudips mexicanus* (Coleoptera: Curculionidae: Scolytinae), in lodgepole pine in British Columbia. *Canadian Entomologist*, **141**, 56–69.
- Stephen, F.M. (2011) Southern pine beetle population dynamics in trees. *Southern Pine Beetle II* (ed. by R. N. Coulson and K. D. Klepzig), pp. 51–74. USDA – Forest Service, Southern Research Station, Asheville, North Carolina.
- Swaine, J.M. (1911) Some insects of larch. *Annals of the Entomological Society of Ontario*, **41**, 81–88.
- Thompson, S.N. & Bennett, R.B. (1971) Oxidation of fat during flight of male Douglas-fir beetles, *Dendroctonus pseudotsugae*. *Journal of Insect Physiology*, **17**, 1555–1563.
- Venette, R.C. & Walter, A.J. (2008) Connecting overwintering success of eastern larch beetle to health of tamarack. *Forest Health Monitoring: 2008 National Technical Report* (ed. by K. M. Potter and B. L. Conkling), pp. 167–169. General Technical Report SRS-158. USDA – Forest Service, Southern Research Station, Asheville, North Carolina.
- Vité, J.P. & Rudinsky, J.A. (1957) Contribution toward a study of Douglas fir beetle development. *Forest Science*, **3**, 156–167.
- Wagner, T.L., Gagne, J.A., Sharpe, P.J.H. & Coulson, R.N. (1983) A biophysical model of southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae), development. *Ecological Modelling*, **21**, 125–147.
- Waring, K.M., Reboletti, D.M., Mork, L.A. *et al.* (2009) Modeling the impacts of two bark beetle species under a warming climate in the southwestern USA: ecological and economic consequences. *Environmental Management*, **44**, 824–835.
- Wermelinger, B. & Seifert, M. (1998) Analysis of the temperature dependent development of the spruce bark beetle *Ips typographus* (L.) (Col., Scolytidae). *Journal of Applied Entomology*, **122**, 185–191.
- Wermelinger, B. & Seifert, M. (1999) Temperature-dependent reproduction of the spruce bark beetle *Ips typographus*, and analysis of the potential population growth. *Ecological Entomology*, **24**, 103–110.
- Werner, R.A. (1986) *The Eastern Larch Beetle in Alaska*. Research Paper PNW-357. United States Department of Agriculture – Forest Service, Pacific Northwest Research Station, Fairbanks, Alaska.
- Werner, R.A., Holsten, E.H., Matsuoka, S.M. & Burnside, R.E. (2006) Spruce beetles and forest ecosystems in south-central Alaska: a review of 30 years of research. *Forest Ecology and Management*, **227**, 195–206.
- WIDNR, Wisconsin Department of Natural Resources (2013) *Wisconsin DNR Forest Health 2013 Annual Report*. Wisconsin Department of Natural Resources, Madison, Wisconsin.
- Williams, W.I. & Robertson, I.C. (2008) Using automated flight mills to manipulate fat reserves in Douglas-fir beetles (Coleoptera: Curculionidae). *Environmental Entomology*, **37**, 850–856.
- Wood, S.L. (1982) The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. *Great Basin Naturalist Memoirs*, **6**, 1–1359.

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