entomology & pathology

Mountain Pine Beetle Voltinism and Life History Characteristics across Latitudinal and Elevational Gradients in the Western United States

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Substantial genetic variation in development time is known to exist among mountain pine beetle (*Dendroctonus ponderosae* Hopkins) populations across the western United States. The effect of this variation on geographic patterns in voltinism (generation time) and thermal requirements to produce specific voltinism pathways have not been investigated. The influence of voltinism on fitness traits, body size, and sex ratio is also unclear. We monitored mountain pine beetle voltinism, adult body size, sex ratio, and air temperatures at sites across latitudinal and elevational gradients in the western United States. With the exception of two sites at the coolest and warmest locations, the number of days required to complete a generation was similar. Thermal units required to achieve a generation, however, were significantly less for individuals at the coolest sites. Evolved adaptations explain this pattern, including developmental rates and thresholds that serve to synchronize cohorts and minimize cold-sensitive life stages in winter. These same adaptations reduce the capacity of mountain pine beetle at the warmest sites to take full advantage of increased thermal units, limiting the capacity for bivoltinism within the current realized distribution. Temperature was not correlated with adult size and sex ratio, and size was greatest in host trees other than lodgepole pine (*Pinus contorta* Dougl.). Our results provide baseline information for evaluating population responses in a changing climate.

Keywords: bark beetle, climate change, countergradient variation, *Dendroctonus ponderosae*, phenology

P henology is the study of the timing of life cycle events in relation to seasonal and climatic change. Phenological events can vary from year to year, and knowledge of patterns across years and across the range of a given species is important for understanding local adaptations that may either enable or constrain response in a changing climate. As environmental conditions change across habitats, phenological patterns of thermally driven fitness traits will also change to maintain appropriate seasonality (Roff 1992). Intraspecific patterns in insect phenology therefore evolve through selection on phenotypic traits that result in maximum fitness for a specific environmental condition (Nylin and Gotthard 1998). In insects, adult emergence timing is a common trait that can

vary substantially across environmentally diverse habitats, thereby influencing multiple fitness traits including appropriate synchrony with host plant phenology (van Asch and Visser 2007), mate finding (Calabrese and Fagan 2004), and synchronization of particular life stages with seasonal cues to avoid potential mortality-inducing factors (Danilevskii 1965, Bentz et al. 1991). A main driver of adult emergence timing is development rate, a key fitness trait that results from temperature-dependent processes that can also influence adult size and fecundity (Fox and Czesak 2000, Kingsolver and Huey 2008). The strong correlation between development rate and temperature is well studied and expected to be a major factor influencing insect response to a changing climate (Bale et al. 2002, Logan et al.

2003, Waring et al. 2009). An intuitive assumption is that climate warming will have a generally positive effect on insect populations, resulting in faster development, which may increase the number of generations per year (i.e., voltinism), and earlier adult emergence (Tobin et al. 2008, Jönsson et al. 2009, Altermatt 2010). Climate can impose significant selection pressures on traits such as development time, however, and some insects have adaptations to particular environmental cues that could be constrained in a warming climate. The result could be delayed or unsynchronized adult emergence rather than a simple increase in the number of generations per year (Logan and Bentz 1999, Hoffmann and Sgro 2011, Ellwood et al. 2012). To predict future insect response to changing climatic conditions, baseline information is needed on thermal requirements for specific voltinism pathways, potential mechanisms driving voltinism, and variations in the pathways across an insect's geographic distribution.

The interacting effects of host plant habitat and climate are major determinates of insect geographic distribution. Species that do not currently occupy the full extent of their host niche are considered to be partially limited by climate with the potential for range expansion in a warming environment, predominately in northern latitudes (Bale et al. 2002). A good example of a species limited by climate is the mountain pine beetle (*Dendroctonus ponderosae* Hopkins, Coleoptera: Curculionidae, Scolytinae), a native of western North America that mainly infests and reproduces in live trees within the genus *Pinus*, and successful offspring production often results in the death of the host tree (Amman and Cole 1983, Safranyik and Carroll 2006). Mountain pine beetle has been a significant cause of tree mortality both historically (Evenden and Gibson 1940, Perkins and Swetnam 1996, Taylor et al. 2006) and in recent years (Meddens et al. 2012). The range of mountain pine beetle is expansive, spanning from Baja California Norte, Mexico, to northern British Columbia and western Alberta, Canada, yet suitable pine hosts extend beyond the current northern and southern extents (Bentz et al. 2010, Safranyik et al. 2010). Temperature plays a key role in population success mediated through its effect on development rate, life cycle timing, and acclimation to cold temperatures (Bentz et al. 1991, Safranyik and Linton 1998, Bentz and Mullins 1999), invoking a climatic limitation to the species range (Safranyik 1978). Ongoing changes in climatic conditions are hypothesized to be driving a northward expansion of mountain pine beetle into lodgepole pine (*Pinus contorta* Dougl.) stands in northern British Columbia and the Northwest Territories and east across the Rocky Mountains into stands of a novel host tree, jack pine (*Pinus banksiana* Lamb) in Alberta, Canada (Cudmore et al. 2010, Cullingham et al. 2011, de la Giroday et al. 2012). The northern range expansion of mountain pine beetle can be considered an ongoing process since the postglacial Holocene recolonization of British Columbia, Canada, by lodgepole pine (Godbout et al. 2008) and whitebark pine (*Pinus albicaulis* Engelm.) (Richardson et al. 2002). Although the extent of mountain pine beetle in Canada before glaciation has not been investigated, genetic data support a relatively recent migration into British Columbia, undoubtedly following its host trees over the past 8,000 years (Mock et al. 2007, Cullingham et al. 2012). Reproductive isolation between mountain pine beetle populations that follow historic gene flow barriers in two host tree species in the United States (Bracewell et al. 2010) is another indication of the close relationships among this insect, climate, and host tree habitat.

Like other *Dendroctonus* species, mountain pine beetle has extreme population fluctuations that can be caused by density-independent processes such as weather or delays and nonlinearities in density-dependent processes (Berryman 1982, Martinson et al. 2013). Populations can exist at low levels for many years until triggered by an inciting factor that results in a sharp increase in relative numbers, followed by a population crash as reproduction exceeds the carrying capacity of the environment, host condition changes, or temperature extremes result in high population mortality or unsynchronized life cycles. Inciting factors that can trigger a population irruption in susceptible forests (see Fettig et al. 2014) are difficult to quantify but may include drought (Chapman et al. 2012), favorable weather (Safranyik 1978, Powell and Bentz 2009), and pathogens that stress individual trees (Goheen and Hansen 1993). At high population levels mountain pine beetle can infest and reproduce in *Pinus* trees that are vigorous and have high resin defense capacity, whereas less vigorous trees with relatively poor defense are colonized at low population levels (Boone et al. 2011). Population irruptions in susceptible forests are a by-product of a series of positive feedbacks that allow population size to increase enough that larger trees with more food, but also more defenses, are able to be overcome through sheer numbers of beetles attacking a tree, coined a mass attack (Raffa et al. 2008). Mountain pine beetle has evolved a diverse set of traits and associations that facilitate this feedback process (Bleiker and Six 2007, Progar et al. 2014), including an adaptive phenology that enables cohort synchrony for mass attacks on well-defended trees (Logan and Bentz 1999, Powell and Logan 2005).

To maintain an appropriate phenology across a large climatic range, mountain pine beetle has adapted to local conditions, resulting in strong genetic and phenotypic patterns in development time across the western United States (Bentz et al. 2011). Projected temperature change is predicted to result in disruption of local adaptation in some areas and transformation of currently inhospitable habitats to thermally favorable ones in other areas (Logan and Bentz 1999, Carroll et al. 2004, Hicke et al. 2006). Disruption of local adaptation could manifest as unseasonal and unsynchronized adult emergence, with associated fitness costs, whereas a switch to a thermally favorable habitat could result in increased seasonality and a reduction in the amount of time required to complete a generation, with associated fitness benefits. Mountain pine beetle life cycle timing has historically been reported as univoltine (i.e., one generation per year) at low elevations with a mix of univoltine and semivoltine (i.e., one generation every 2 years) at high elevations (Reid 1962, Amman 1973). The capacity for mountain pine beetle to complete two generations in a single year (i.e., bivoltinism) is unclear. Bivoltinism was reported to have occurred in California (Furniss and Carolin 1977) and is speculated to occur with warming temperatures at 3,000 m in Colorado (Mitton and Ferenberg 2012).

Adult size and population sex ratio are fitness traits with links to voltinism and temperature and, therefore, may also be influenced by climate change. Mountain pine beetle body size is known to be correlated with energy reserves (Graf et al. 2012), pheromone production (Pureswaran and Borden 2003), and reproductive capacity (McGhehey 1971, Elkin and Reid 2005), although not with development time (Bracewell et al. 2013). Sex ratio of emerged mountain pine beetle is female-skewed (Amman and Cole 1983) and may vary during brood adult emergence (Rasmussen 1980). Similar to voltinism pathways in mountain pine beetle, however, variability among populations and the influence of specific thermal regimes and voltinism on body size and sex ratio have not been investigated.
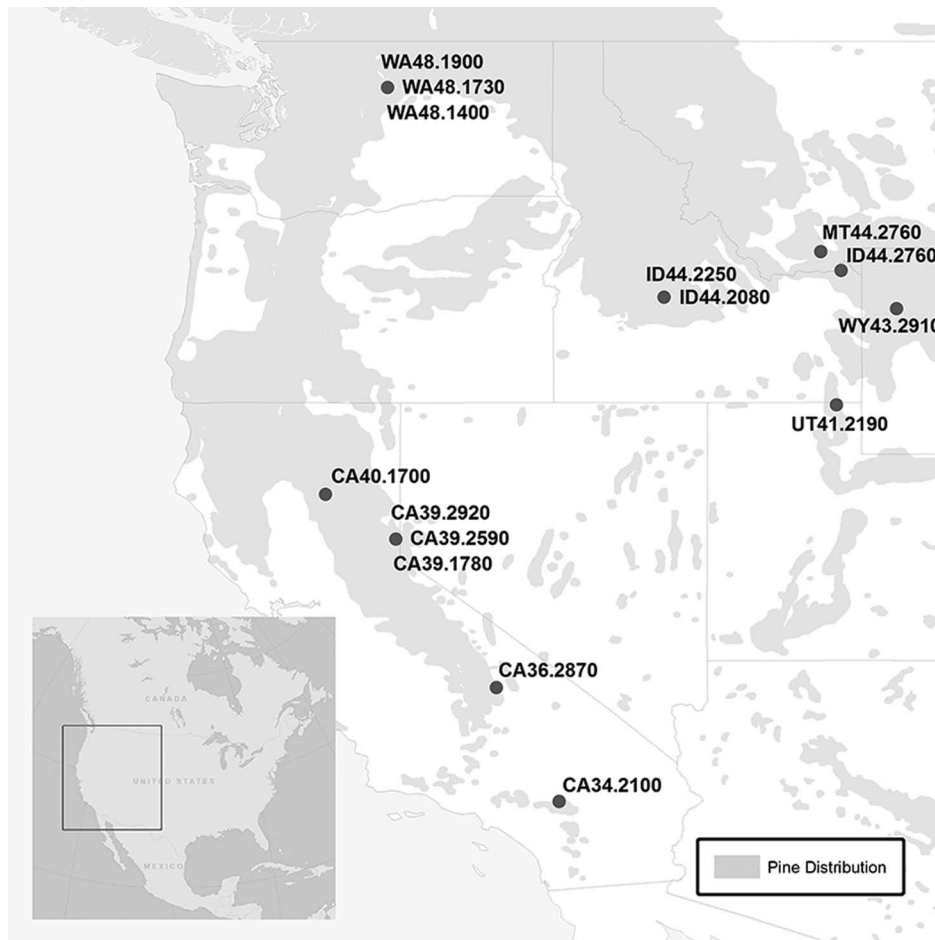
Figure 1. Map of study sites in the western United States. Three areas have sites at different elevations (WA48, CA39, and ID44). Also shown is the distribution (Little 1971) of major pine host species for mountain pine beetle (i.e., *P. albicaulis, P. contorta, P. flexilis, P. lambertiana, P. monticola, P. ponderosa,* and *P. strobiformis*).

Our objectives were to describe mountain pine beetle voltinism, adult size, sex ratio, and associated air temperatures across latitudinal and elevational gradients in the western United States, including warm habitats with the potential for bivoltinism. This information will provide a baseline for evaluating potential future population responses to changing climate and help identify areas with a high probability of climate-induced shifts in population success where management interventions may be most effective.

Methods
Study Sites
Study sites were identified by locating areas with active mountain pine beetle populations and reasonable road access. We attempted to establish multiple sites within an area at different elevations and with multiple host tree species, although this was not always possible. Data from 15 sites located across the western United States are included in this study (Figure 1), with information on two mountain pine beetle generations and associated air temperatures collected at most sites (Table 1). Three areas have sites at different elevations (WA48, CA39, and ID44). Site names reflect geographic location and are a combination of the state abbreviation, latitude, elevation, and year of mountain pine beetle attack. For example, CA39.2920-09 is a site in California located at approximately 39° latitude and 2,920 m elevation, and the year of attack was 2009 (Table 1). Ambient air temperature was measured at each site using

one radiation-shielded temperature probe placed at 1.4 m above the ground on the north side of a tree to reduce direct sun exposure (Campbell Scientific, Inc, Logan, UT; Onset Corporation, Bourne, MA). Hourly air temperature was continuously recorded and stored for each site from the beginning of parent adult attacks through the end of brood adult emergence. At each site, dbh (cm) of each sample tree was recorded (Table 1).

Temperature-Dependent Voltinism
Mountain pine beetle adults emerge from trees and fly to attack new live trees where mating and oviposition occur, and new brood will develop within the phloem throughout the next 1−2 years. The timing of emergence and flight is dependent on temperature and typically occurs in the summer months (Safranyik and Carroll 2006). We define a brood to be a group of individuals that develop from eggs laid by parents that attacked trees in the same season. The length of time for brood to develop and emerge from a tree is considered a generation. Brood that emerged from a tree the summer after parent attacks were classified as univoltine (i.e., completion of a generation in 1 year), and semivoltine brood required 2 years to complete a generation. To be considered a bivoltine brood, 2 complete generations must occur within 1 year (Torre-Bueno 1978).

Before mountain pine beetle flight, 3−5 live trees were selected at each site based on tree size (>20.2 cm dbh). To ensure mountain

Table 1. Study site location, years the site was sampled, mountain pine beetle population phase, and *Pinus* host tree species.

State	USDA National Forest	Site name	Years	Population phase	Dbh (mean ± SD)	Latitude	Longitude	Elevation (m)	Host tree species
WA	Okanogan-Wenatchee	WA48.1900-09	2009–2011	Epidemic	26.67 ± 4.1	48.1001	−120.2442	1,900	*P. albicaulis*
WA	Okanogan-Wenatchee	WA48.1900-10	2010–2012	Epidemic	35.81 ± 0.8	48.0981	−120.2438	1,900	*P. albicaulis*
									P. contorta
WA	Okanogan-Wenatchee	WA48.1400-09	2009–2011	Epidemic	28.7. ± 3.8	48.1181	−120.2259	1,400	*P. contorta*
WA	Okanogan-Wenatchee	WA48.1400-10	2010–2011	Epidemic	27.69 ± 1.3	48.1176	−120.2197	1,400	*P. contorta*
WA	Okanogan-Wenatchee	WA48.1730-09	2009–2011	Epidemic	30.48 ± 5.3	48.0977	−120.2597	1,730	*P. contorta*
WA	Okanogan-Wenatchee	WA48.1730-10	2010–2012	Epidemic	31.50 ± 6.1	48.0967	−120.2615	1,730	*P. contorta*
ID	Sawtooth National Recreation Area	ID44.2080-01	2001–2002	Epidemic	na	44.1450	−114.8942	2,080	*P. contorta*
ID	Sawtooth National Recreation Area	ID44.2250-01	2001–2002	Epidemic	na	43.8651	−114.8104	2,250	*P. contorta*
MT	Beaverhead-Deerlodge	MT44.2760-03	2003–2005	Epidemic	38.35 ± 7.8	44.9242	−111.8350	2,760	*P. albicaulis*
MT	Beaverhead-Deerlodge	MT44.2760-04	2004–2006	Epidemic	41.40 ± 7.1	44.9242	−111.8350	2,760	*P. albicaulis*
ID	Caribou-Targhee	ID44.2760-03	2003–2005	Epidemic	50.29 ± 7.9	44.5558	−111.4416	2,760	*P. albicaulis*
ID	Caribou-Targhee	ID44.2760-04	2004–2006	Epidemic	48.01 ± 6.9	44.5558	−111.4416	2,760	*P. albicaulis*
WY	Shoshone	WY43.2910-03	2003–2005	Epidemic	45.21 ± 5.1	43.7436	−110.0513	2,910	*P. albicaulis*
WY	Shoshone	WY43.2910-04	2004–2006	Epidemic	46.74 ± 8.6	43.7436	−110.0513	2,910	*P. albicaulis*
UT	Uinta-Wasatch-Cache	UT41.2190-10	2010–2012	Endemic	53.85 ± 14.9	41.9528	−111.5290	2,190	*P. contorta*
UT	Uinta-Wasatch-Cache	UT41.2190-11	2011–2012	Endemic	42.16 ± 7.1	41.9529	−111.5294	2,190	*P. contorta*
CA	Lassen	CA40.1700-09	2009–2010	Endemic	50.55 ± 6.4	40.2238	−121.4331	1,700	*P. lambertiana*
CA	Lassen	CA40.1700-10	2010–2011	Endemic	39.37 ± 8.6	40.2103	−121.4341	1,700	*P. lambertiana*
CA	Tahoe	CA39.1780-09	2009–2010	Endemic	33.27 ± 5.3	39.3926	−120.1841	1,780	*P. contorta*
CA	Tahoe	CA39.1780-10	2010–2011	Endemic	33.78 ± 6.1	39.3922	−120.1863	1,780	*P. contorta*
CA	Lake Tahoe Basin Mgmt. Unit	CA39.2590-09	2009–2011	Endemic	46.74 ± 8.1	39.2984	−119.9330	2,590	*P. monticola*
									P. contorta
CA	Lake Tahoe Basin Mgmt. Unit	CA39.2590-10	2010–2012	Endemic	44.96 ± 4.6	39.2998	−119.9310	2,590	*P. monticola*
									P. contorta
CA	Lake Tahoe Basin Mgmt. Unit	CA39.2920-09	2009–2012	Endemic	33.53 ± 2.8	39.3218	−119.9390	2,920	*P. albicaulis*
CA	Lake Tahoe Basin Mgmt. Unit	CA39.2920-10	2010–2012	Endemic	39.12 ± 3.1	39.3217	−119.9386	2,920	*P. albicaulis*
									P. contorta
CA	Inyo	CA36.2870-09	2009–2010	Endemic	43.43 ± 18.5	36.4693	−118.1252	2,870	*P. flexilis*
CA	Inyo	CA36.2870-10	2010–2011	Endemic	47.24 ± 19.6	36.4695	−118.1253	2,870	*P. flexilis*
CA	San Bernardino	CA34.2100-09	2009–2010	Endemic	50.89, 46.2	34.2653	−116.9089	2,100	*P. monophylla*
CA	San Bernardino	CA34.2100-10	2010–2011	Endemic	33.27	34.2635	−116.9087	2,100	*P. monophylla*

Population phase was determined based on field observations in the general area during the first site visit. Endemic sites had 1–5 infested trees/ha and epidemic sites had >5 infested trees/ha. Site names are a combination of the state abbreviation, approximate latitude, elevation (m), and parent attack year and are arranged by latitude with the most northerly sites at the top. Also shown is the mean ± SD dbh of trees sampled at each site. dbh was not available at two sites.

pine beetle attacks, an aggregation lure [(S)-*trans*-verbenol and racemic *exo*-brevicomin; Synergy Semiochemicals Corporation, Burnaby, BC, Canada] was placed on each live tree when mountain pine beetle flight activity was observed in the area (based on pheromone traps and emergence cages in the vicinity). Aggregation lures were removed once attacks were initiated on each tree to allow the natural attack process to continue. Beetle attacks were monitored either daily or twice weekly on the entire circumference of each tree bole from 0.305 to 1.524 m aboveground until attacks ceased. At the WA48.1900, ID44.2760, MT44.2760, WY43.2910, and CA36.2870 sites aggregation lures were not used, and only the general timing of peak attack was recorded.

After the entire circumference of each tree bole was successfully mass attacked, emergence cages were installed, centered at 1.4 m above the ground. To describe within-tree variability in emergence timing, sex ratio, and adult size, cages were installed on the north and south bole aspects of each tree. Cages were 31 × 61 cm in size and constructed from flexible nylon screen with a mesh size sufficiently small to prevent adult beetle escape. Cages were stapled onto the tree bole, covering a standardized portion of each bole. A centrifuge tube attached to the bottom of the enclosure collected all beetles emerging from under the bark within each cage. Adult mountain pine beetle emergence into cages was monitored at least twice weekly at each site. At CA34.2100-09, cages were not placed on one tree before emergence commenced, and emergence holes observed before the cage was installed were also used as a measure of adult beetle emergence timing. At most sites, the process was repeated for a second brood using new live trees located within 500 m of the previous plot. Parent attacks on the new live trees, brood emergence in subsequent years, and associated air temperatures were monitored as described above for the first brood. Cages were left on trees at CA39.2920-09, CA39.2920-10, CA39.2590-10, UT41.2190-10, and UT41.2190-11 for at least 2 years after parent attacks to capture potential emergence of semivoltine brood.

Adult Size and Sex Ratio

Adults were collected from emergence cages, labeled by site, tree number, bole aspect, and date and then frozen before shipment to Logan, Utah. Sex of emerged brood adults was determined (Lyon 1958), and pronotum width was measured for each collection day. Sex ratio was calculated as the ratio of males to females by collection day and averaged across all days to determine the mean sex ratio of emerged adults at each site. Adult sex and size were not determined for beetles collected from the ID44.2760, MT44.2760, WY43.2910, ID44.2250, and ID44.2080 sites.

Statistical Analyses

To test the influence of air temperature on generation time and the timing of brood adult emergence and flight, hourly air temperature data were summarized as accumulated degree-days (DD) determined by integration) and the number of hours (DH) above a range of published threshold temperatures. To test for the influence of temperature on generation time, accumulated DD above each

Table 2. Proportion brood that emerged in 1 (univoltine) year, the associated total number of brood adults sampled from cages (*N*), sex ratio (male:female), generation time, and temperature metrics at each site.

Site	Proportion univoltine (*N*)	Generation sex ratio: year 1/year 2	Generation time (days)	DD >15° C	Annual air	July–Aug. maximum air	Dec.–Jan. minimum air
						Average temperature	
WA48.1900-09[a]	78.7 (150)	1:1.84/1:1.83			1.5	16.6	−8.0
WA48.1900-10[a]	100.0 (122)	1:1.84			2.0	16.8	−6.6
WA48.1730-09	100.0 (169)	1:2.53			2.1	17.3	−7.7
WA48.1730-10	100.0 (1,402)	1:1.82	383	69.41	2.3	17.0	−6.9
WA48.1400-09	100.0 (362)	1:1.68			2.6	20.6	−9.1
WA48.1400-10	100.0 (159)	1:1.70	365	133.5	3.6	21.3	−7.2
MT44.2760-03[a]	13.3 (1,023)	.					
MT44.2760-04[a]	52.1 (562)				0.1	17.2	−10.2
ID44.2760-03[a]	68.8 (269)						
ID44.2760-04[a]	55.2 (788)				0.0	16.8	−11.0
ID44.2250-01	100.0 (1,400)				2.1	14.3	−9.1
ID44.2250-02	100.0 (185)						
ID44.2080-01	100.0 (1,173)				2.7	15.0	−8.8
ID44.2080-02	100.0 (920)						
WY43.2910-03[a]	18.8 (772)						
WY43.2910-04[a]	48.2 (879)				−0.4	17.7	−11.8
UT41.2190-10[a]	87.1 (279)	1:1.56/1:2.27	372	244.04	1.7	23.9	−11.6
UT41.2190-11	100.0 (209)	1:1.64	351	293.62	3.0	25.6	−14.0
CA40.1700-09	100.0 (32)	1:1.73	368	365.95	5.9	25.2	−3.9
CA40.1700-10	100.0 (101)	1:2.05	338	231.37	6.2	24.0	−2.8
CA39.2920-09[a]	64.2[c] (944)	1:1.27/1:1.60	402	86.27	1.3	16.8	−8.4
CA39.2920-10[a]	13.8 (319)	1:3.00/1:2.13	695	74.59	1.2	16.3	−7.1
CA39.2590-09	100.0 (616)	1:1.24	388	166.20	3.3	21.3	−6.6
CA39.2590-10[a]	71.5 (884)	1:1.84/1:1.76	385	110.16	2.4	19.1	−6.2
CA39.1780-09	100.0 (454)	1:1.73	393	447.00	5.0	25.8	−8.7
CA39.1780-09	100.0 (863)	1:1.73	371	371.32	4.5	26.2	−8.1
CA36.2870-09	100.0 (968)	1:1.07			4.4	20.6	−7.5
CA36.2870-10	100.0 (839)	1:1.47			4.6	20.5	−5.7
CA34.2100-09 T2	4.0[b] (170)		110	484.16	8.8	27.0	−3.8
CA34.2100-09 T5	100.0 (176)		295	288.75	8.8	27.0	−3.8
CA34.2100-10	100.0 (69)				8.1	25.7	−3.7

Sites are arranged with the most northerly at the top (see Table 1 for site information). Site name includes the state abbreviation, approximate latitude, elevation, and year of parent attacks. Site CA34.2100 also includes sample tree number. The sex ratio (male:female) of emerging adults was measured separately for beetles emerging in 1 and 2 years. Generation time is the number of days between median attack and median emergence, information available for a portion of the sites. DD >15° C is the accumulated degree-days >15° C between median attack and median emergence. Average annual temperature, average daily maximum air temperature in July and August, and average daily minimum air temperature in December and January were calculated using sensors located at each site.

[a] Remainder of brood emerged >1 year after attacks.
[b] Remainder of brood emerged <1 year after attacks.
[c] 1.1% emerged in 3 years.

threshold was calculated between the date of median attack and the date of median emergence at a site, using threshold temperatures of 5.6, 12, and 15° C. The lowest temperature for mountain pine beetle development is 5.6° C, and this temperature is often used as a base temperature for DD (Bentz et al. 1991, Safranyik and Carroll 2006). Temperatures near 15° C are believed to be required for pupation (Bentz et al. 1991, Régnière et al. 2012). This threshold may vary geographically (Safranyik and Carroll 2006), however, so we also tested 12° C. Only those sites where parent attacks were monitored regularly and generation time could be accurately calculated were included in this analysis (Table 2). Linear regression was used to test for differences in accumulated DD required for completion of a generation among sites as a function of the site latitude and elevation.

To test temperature as a cue for brood adult emergence, DH above 12, 15, and 18° C for 2, 5, and 10 days before daily emergence was calculated based on previously described thresholds for different locations within the range of mountain pine beetle (Reid 1962, Amman and Cole 1983, Safranyik and Carroll 2006). Pearson's partial correlation coefficients were calculated for each temperature

threshold-day combination and the number of emerged adults. DH-day combinations with the highest correlation were included in analyses. Emergence timing was estimated as the relative number of adults that emerged into cages by Julian date (JD). Mixed models were used to describe the influence of JD, DH-day accumulations, daily maximum and minimum temperature, and tree bole aspect on the number of emerged univoltine adults. The same analysis was conducted using data for sites with both univoltine and semivoltine brood, and voltinism was included as an additional fixed effect.

Mixed models were also used to test for differences in adult size (pronotum width, mm) as a function of the fixed effects sex, tree bole aspect, dbh, emergence period, DH accumulations, maximum and minimum temperature, and voltinism. To standardize among the sites, adult size data were summarized by week of the emergence period. The first date that individuals were observed in cages was considered the first week. Week data were further summarized into 4 quantiles by dividing the total number of weeks of emergence into 4 equal time periods, referred to as emergence period hereafter, by emergence year. At sites with more than one host tree species, the effect of tree species on adult size was also tested. Site and tree, and

interactions between these random and the fixed effects, were considered random. Post hoc pairwise comparisons were conducted with Tukey's honestly significant difference test. Effect of the random variable site on adult size was tested using best linear unbiased predictions (BLUPs) that incorporate the random effect into the estimation of the mean for a particular site (Littell et al. 1996). Differences in sex ratio among emergence periods were tested using mixed models with site included as a random effect and a binomial distribution. All analyses were conducted using SAS (version 9.3; SAS Institute, Inc., Cary, NC).

Results

Temperature-Dependent Voltinism

Mountain pine beetle life cycle timing and air temperature varied among sites and among years at the same site (Table 2; Figures 2 and 3). A strictly univoltine life cycle was observed at 61% of the sites for a given attack year, 35% had a mixture of univoltine and semivoltine brood (often within the same tree), and the warmest site produced brood in less than 1 year (Table 2). At the warmest site, CA34.2100-09, some brood adults emerged from a single tree (T2) the fall after attacks earlier that summer. Attacks were first observed on T2 on June 28, 2009, and 96% of the adults emerged before Nov. 23, 2009 and the remaining 4% emerged the following May and June. Median attacks on a second tree (T5) at the CA34.2100-09 site occurred on Oct. 2, 2009, coinciding with emergence from T2, and peak brood adult emergence from this tree was on July 24, 2010 (Figure 2). The majority of brood from parents that laid eggs in June completed a generation by the first fall (faster than univoltine). To be classified as bivoltine, however, brood from attacks made by these emerging adults in fall 2009 would need to have completed development and emerged by June 2010 (i.e., two complete generations in a single year). This did not happen. The next generation at CA34.2100 was initiated from attacks that occurred in July and August 2010. Brood from these attacks emerged in July 2011, a strictly univoltine life cycle. Therefore, the CA34.2100 site produced three generations in 2 years, a fractional voltinism faster than strict univoltinism but not bivoltinism (Figure 2).

At the opposite extreme was the highest elevation site, CA39.2920, where 1.1% of offspring from attacks in 2009 emerged in 2012, a life cycle that required 3 years to complete (Figure 2). The coolest sites tended to produce a mixture of univoltine and semivoltine beetles, although the proportions varied each year among sites and among years within a site (Table 2). For example 64.2% of brood from trees attacked in 2009 at the CA39.2920 site emerged in 1 year, and at this same site in 2010 (CA39.2920-10) only 13.8% emerged the first year. The summer and fall of 2009 were much warmer than those seasons in 2010, and brood developing in trees attacked in 2009 experienced 300 more accumulated DH >15° C the first year compared with brood developing in trees attacked in 2010. Similar results were seen at three high elevation sites in Idaho (ID), Montana (MT), and Wyoming (WY) (ID44.2760, MT44.2760, and WY43.2910) where a low proportion of univoltine brood emerged from trees attacked in 2003 compared with trees attacked in 2004 (Table 2). We also observed relatively late fall emergence at several high-elevation sites. For example, at CA39.2590-10, 73 adults emerged between Sept. 28 and Oct. 18, 2011, when cages were last checked, and an additional 143 dead adults were found in cages on May 23, 2012; most likely they had emerged late the previous fall. The fate of other fall-emerging adults is unknown as we observed no new attacked trees.

We monitored sites from 34.2° to 48.1° latitude across an elevational range from 1,341 to 2,926 m. Elevation and latitude were poor predictors of generation time (i.e., number of days between median attack and median emergence) ($R^2 = 0.4037$). Comparatively, elevation and latitude were good predictors of total DD above all threshold temperatures (5.6, 12, and 15° C), although the most variation was explained for 15° C, the approximate threshold for pupation ($R^2 = 0.7409$) (Table 3). We then developed a proxy for site that incorporated the influence of latitude and elevation on DD >15° C to complete a generation. Elevation-corrected latitude was calculated for each site as effective latitude (L_E) = latitude + elevation/k, where k is a conversion factor calculated as the quotient of the regression coefficients for latitude and elevation ($k = -28.8575/-0.223017 = 129.4$) that explain DD >15.0° C (Table 3) (see Bradshaw and Lounibos 1977). Therefore, an increase in 129.4 m elevation has an effect on DD >15° C required for completion of a mountain pine beetle generation equal to that of an increase in latitude of 1° N. We then used this conversion factor to calculate an L_E for each site.

Across all sites, the average DD >15° C for completion of a generation was 240.5 ± 139.9 DD, and the average number of days was 373.6 ± 110.3 days. With the exception of two sites at the lowest and highest L_E, generation time was not influenced by L_E (Figure 4A). Conversely, thermal heat required for completion of a generation decreased significantly as L_E increased (Figure 4B). The majority of individuals at CA34.2100-09 T2 ($L_E = 50.6$) completed development by the fall of the attack year (110 days), and 484.16 DD >15° C were accumulated during the generation time. The majority of individuals at CA39.2920-10 ($L_E = 61.9$) required 2 years to complete a generation (695 days), yet only 74.59 DD >15° C were required to complete the generation.

Temperature Thresholds for Emergence

Emergence timing was estimated as the relative number of adults that emerged into cages by JD. We were interested in determining temperature thresholds for flight and whether emergence timing and thresholds differed among voltinism types or tree bole aspect. Emergence timing differed among the sites and years but was not significantly influenced by aspect or JD × aspect for either univoltine or semivoltine beetles (Table 4). These results also indicate that the total number of univoltine and semivoltine brood emerged did not differ by tree bole aspect. The only thermal summation variables found to be significant in predicting adult emergence timing of univoltine brood were DH >15° and DH >18° C for 2 days before the date of emergence, and these models had similar Akaike information criterion values. Daily maximum temperature on the day samples were collected was also significant in predicting number of univoltine beetles. When sites with both semivoltine and univoltine beetles are included, voltinism type was highly significant. DH >15° C for 5 days before emergence and maximum temperature on the day samples were collected were also significant, although DH >15° C before emergence provided a slightly better model fit based on Akaike information criterion values (Table 4). Semivoltine beetles emerged significantly earlier than univoltine beetles and overall had less accumulated DH before emergence and lower daily maximum temperature on the day of emergence (Table 4; Figure 5). A small proportion of both semivoltine and univoltine beetles emerged in the early summer and late fall when temperatures were
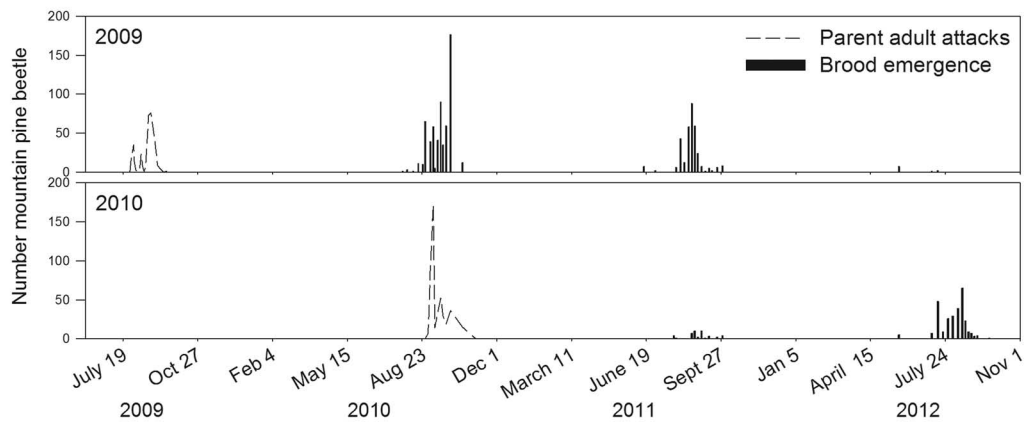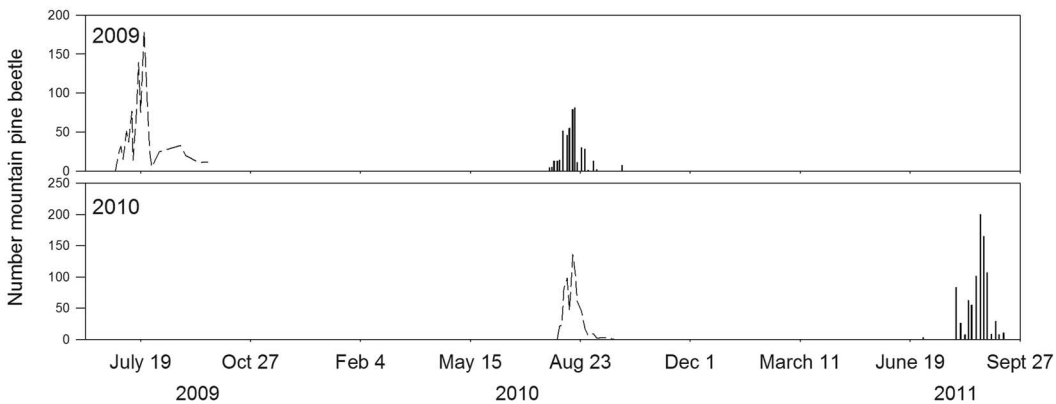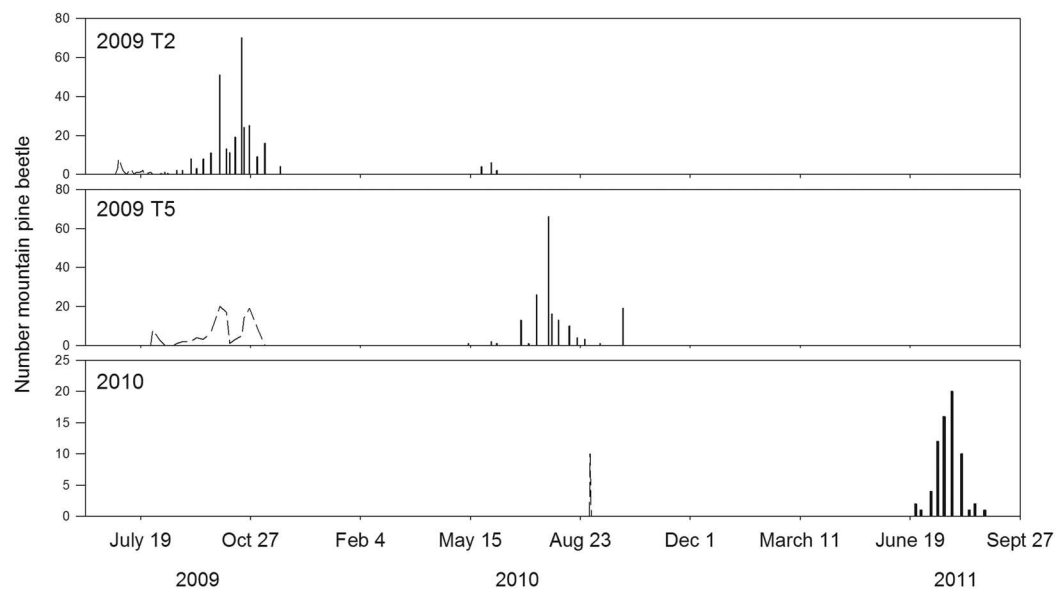
Figure 2. Mountain pine beetle attack and emergence timing across all trees at 3 sites. (A) CA39.2920-09 produced a mix of univoltine brood that emerged in 2010, semivoltine brood that emerged in 2011, and a small number of brood that required 3 years. CA39.2920-10 produced a mix of univoltine and semivoltine brood. (B) Strictly univoltine brood were produced at CA39.1780-09 and CA39.1780-10. (C) Two trees were attacked at different times at the CA34.2100-09 site. T2 was attacked in late June and some brood emerged later that same year. CA34.2100-09 T5 and CA34.2100-10 produced univoltine brood. Note the differences in scale on the x axis. See Table 1 for site information.

$<15°$ C (Figure 5). There was considerable overlap in the emergence timing of the two voltinism types, although there was an average of 35 days between median emergence of univoltine and semivoltine beetles at a site.

Adult Size and Sex Ratio

Based on BLUP estimates for the random effect site, there were differences in adult size among sites, but L_E and temperature variables were not significant in explaining these differences. With the
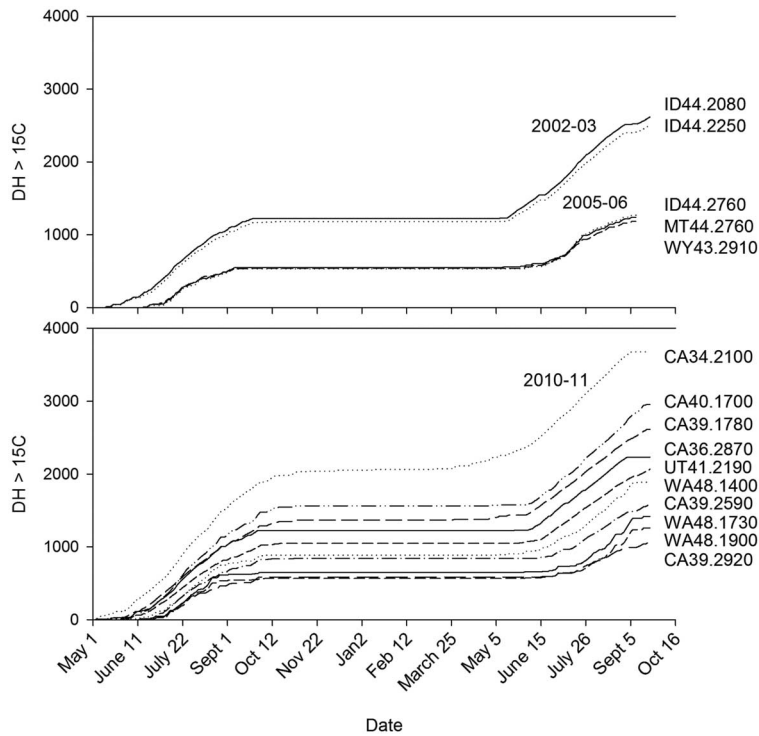
Figure 3. Cumulative DH >15° C accumulated between May 1 and September 30 in the year after attack at each site. The top panel shows sites monitored in 2002–2006, and the bottom panel shows sites monitored in 2010−2011. See Table 1 for site information.

Table 3. Effect of latitude and elevation of 15 sites on accumulated DD required to complete a generation (median attack to median emergence) above temperature thresholds 5.6, 12.0, and 15.0° C.

Effect	Estimate	F	P	R^2	Mean ($\pm$SD)
DD >5.6° C				0.4766	1102.9 (242.2)
Latitude	−43.9216	5.46	0.0394		
Elevation	−0.2571	4.56	0.0561		
DD >12.0° C				0.7190	421.8 (180.2)
Latitude	−37.2711	10.46	0.0079		
Elevation	−0.2762	17.69	0.0015		
DD >15.0° C				0.7409	240.5 (139.9)
Latitude	−28.8575	23.66	0.0005		
Elevation	−0.2230	20.74	0.0008		

Also shown is the mean ($\pm$SD) of the estimated DDs above each temperature threshold to complete a generation across the sites.

exception of UT41.2190, adults from sites with five-needle pine or single-leaf pinyon (*Pinus monophylla* Voss) hosts were the largest, and beetles from sites with only lodgepole pine were the smallest (Table 1; Figure 6). Females were significantly larger than males at all sites, regardless of the voltinism type (Table 5). Univoltine beetles that emerged from larger trees were bigger, although adult size from north and south bole aspects did not differ significantly (Table 5). Adult size of univoltine beetles differed significantly by emergence period, with a general trend for adults that emerged later in the year to be smaller than those that emerged earlier (Table 5). This trend was strongest on the south bole aspect where adults were significantly smaller at the end of the emergence period than at the first ($t_{88.98}$ = 3.71, adjusted P = 0.0143) and second (t_{66} = 3.35, adjusted P = 0.0362) periods. Semivoltine beetles were significantly smaller than univoltine beetles (Table 5), although the difference was mostly due to beetles emerging from the south bole aspect. Semivoltine beetles emerged from south bole aspects were signifi-

cantly smaller than semivoltine beetles emerged from north bole aspects ($t_{57.87}$ = 5.22, adjusted P < 0.0001) and univoltine beetles from both north ($t_{59.11}$ = 6.06, adjusted P < 0.0001) and south ($t_{227.1}$ = 5.67, adjusted P < 0.0001) aspects.

Sex ratio of emerged brood adults ranged from an almost equal sex ratio at the CA36.2870-09 site (1:1.07) to a highly female-skewed ratio in univoltine beetles at the CA39.2920-10 site (1:3.00) (Figure 7; Table 2). Sex ratio tended to favor females at sites with the lowest accumulated heat (i.e., highest L_E) and in semivoltine brood and was lowest (i.e., fewer males) at sites where the total number of beetles emerged was also the lowest ($F_{1, 13.41}$ = 4.40, P = 0.0553). Although sex ratio was highly variable, it did not differ significantly among tree bole aspects or emergence period in either univoltine or semivoltine beetles. Across all sites, we did not observe a consistent trend for either males or females to emerge first (Figure 7).

Effect of Host Tree Species at a Site

The majority of sites had a single host tree species, although at two sites, CA39.2590 and CA39.2920, other *Pinus* species were attacked. At the CA39.2590 site, attacked lodgepole pine and western white pine (*Pinus monticola* Dougl.) were monitored, and lodgepole pine and whitebark pine were followed at the CA39.2920 site. At these sites, sizes of male and female beetles that emerged from either western white pine or whitebark pine were significantly larger than those of adults from lodgepole pine (host tree: $F_{2, 10.71}$ = 7.01, P = 0.0113; sex: $F_{1, 34.86}$ = 379.67, P < 0.0001; host × sex: $F_{2, 34.83}$ = 2.41, P = 0.1043), although dbh was not significant. There was no significant difference in total number of emerged adults between host tree species and dbh (host tree: $F_{2, 8.93}$ = 8.93, P = 0.7525; dbh: $F_{1, 8.33}$ = 4.98, P = 0.0549; dbh × host tree: $F_{2, 8.74}$ = 0.12, P = 0.8849).
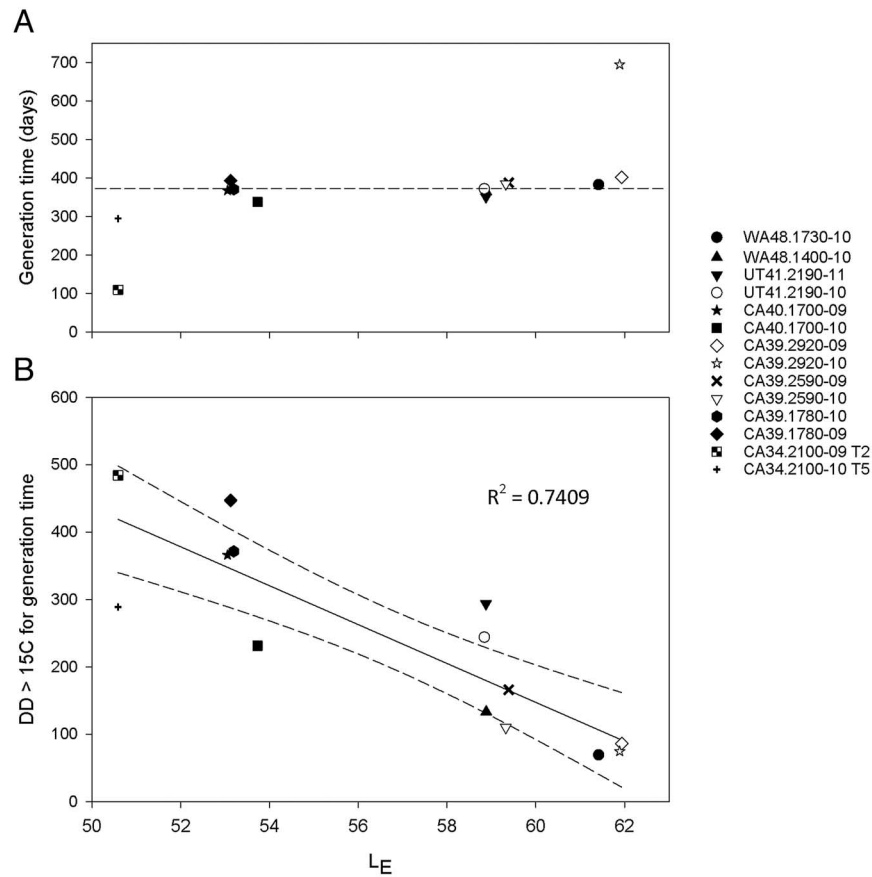
Figure 4. Generation time (number of days between median attack and median emergence) of mountain pine beetle as a function of site L_E (A), and DD $>15°$ C required to complete a generation at each site as a function of L_E (B). High L_E sites are at effectively higher elevation and/or latitude. Open symbols represent sites with a mix of univoltine and semivoltine brood, closed symbols represent those with only univoltine brood, and the closed/open symbol is a site with brood that developed in <1 year. Average generation time is shown as a dashed line in panel A and 95% confidence intervals are shown as a dashed line in panel B. See Table 1 for site information.
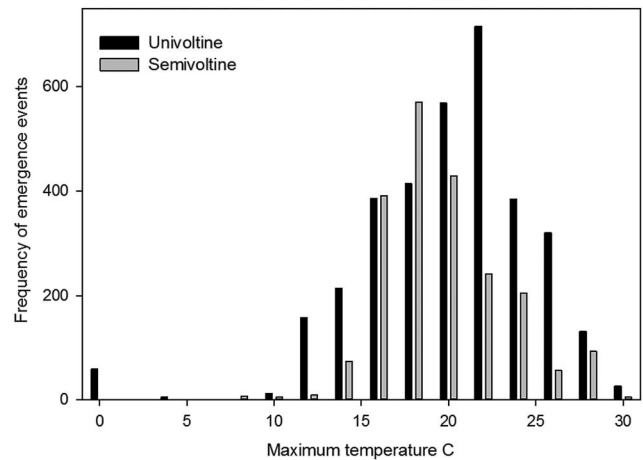
Table 4. Mixed model results testing the effect of tree bole aspect, JD, DH $>15°$ C for 2 days before emergence, daily maximum temperature on the date of emergence, dbh, and voltinism type (i.e., univoltine or semivoltine) on emergence timing estimated as the number of emerged adults by JD.

Effect	Num, Den df	F	P
Univoltine only			
Aspect	1,1,187	2.30	0.1295
JD	1,1,166	15.25	<0.0001
JD $\times$ aspect	1,1,186	1.70	0.1920
DH $> 15°$ C 2 days	1,1,215	14.78	0.0001
Daily maximum temperature	1,1,013	8.96	0.0028
Univoltine and semivoltine			
Aspect	1,407.0	0.01	0.9410
JD	1,411.6	1.89	0.1702
Voltinism	1,409.5	14.74	0.0001
DH $>15°$ C 5 days	1,412.5	17.71	<0.0001
JD $\times$ aspect	1,407.0	0.00	0.9618
JD $\times$ voltinism	1,410.0	16.15	<0.0001
JD $\times$ aspect $\times$ voltinism	1,407.0	0.24	0.6245
Aspect $\times$ voltinism	1,407.0	0.00	0.9410
DH $>15°$ C 5 days $\times$ voltinism	1,407.2	4.67	0.0314

Num, numerator; Den, denominator.

Figure 5. Frequency of the number of mountain pine beetle emergence events, weighted by the number of mountain pine beetle emerged, as a function of maximum daily temperature (° C) on the date of emergence for univoltine and semivoltine beetles. Only sites with both voltinism types are included.

Discussion

With the exception of two sites at the warmest and coldest locations, we found that the median generation time across a range of latitude and elevation (L_E from 50.6 to 61.9) was surprisingly sim-

ilar (373 days), even though several sites produced a mix of univoltine and semivoltine brood and others produced only univoltine brood (Table 2; Figure 4A). Common garden laboratory studies, however, have shown that mountain pine beetle populations that
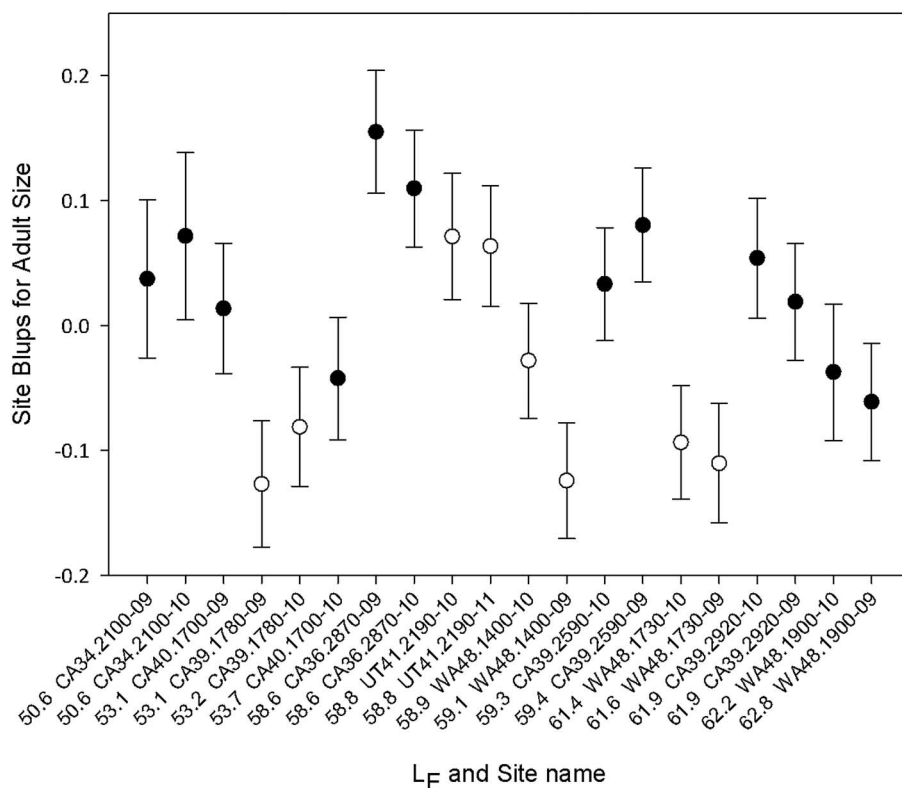
Figure 6. BLUP (± SE) of adult size for each site and associated L_E that describes the relationship between elevation and latitude and DD required to complete a generation. Sites with lodgepole pine are shown with open symbols and sites with other pine host tree species are shown in black. See Table 1 for site and host tree information.

have evolved in cooler northern latitudes develop faster than beetles evolved at warmer lower latitudes, an indication that local adaptation resulting in genetic differences in development time occurs (Bentz et al. 2011, Bracewell et al. 2013). A comparison of results from the laboratory and field suggests that similar developmental phenotypes observed in the field (i.e., similar generation time) may not necessarily translate to similar genotypes, an indication of countergradient variation in development time (Conover and Schultz 1995). Countergradient variation, in which genetic and environmental influences on a trait oppose each other along a geographic gradient, can conceal evolutionary response at the phenotypic level (Merilä 2012). This is important to consider in the geography of adaptive genetic variation and when making predictions about climate change-induced population response in insects with an expansive range. Geographically and genetically distinct populations with a similar development time in the field may respond differently to a changing climate. Note that our sampling was limited to the western United States. Although mountain pine beetle populations in western Canada have similar voltinism pathways (Reid 1962), potential differences in local adaptation could result in different thermal regimes driving voltinism in western Canada.

Our results support previous findings that mountain pine beetle life cycle timing is univoltine at warmer sites and a mix of univoltine and semivoltine at cooler sites (Reid 1962, Amman 1973) and provide insight into thermal regimes that result in specific voltinism pathways. Although generation time was similar among the majority of sites, the thermal units required to complete a generation differed markedly. The cooler the site (i.e., higher L_E), the fewer thermal units needed for completion of a generation regardless of

the number of days (Figure 4B). One explanation for this pattern involves development rates and differences among life stages in thermal thresholds for development. The peak mountain pine beetle development rate in all life stages occurs around 25° C, although temperature thresholds for development vary among the life stages (Régnière et al. 2012). Temperatures >5.6° C are required for development of eggs and early instars, and temperatures >15° C are required for later instars and pupation (Safranyik and Whitney 1985, Régnière et al. 2012). These life stage-specific development thresholds play important roles in enabling univoltinism and brood adult emergence synchrony (Bentz et al. 1991, Powell and Logan 2005), two traits important to population success (Safranyik 1978, Logan and Bentz 1999). Moreover, genetic differences in response to temperature among latitudinally separated populations highlight how physiological adaptations to local environments serve to maintain these life history strategies across the range of this insect in the western United States (Bentz et al. 2011). Results from this study suggest that evolved adaptations that promote univoltinism and emergence synchrony allow populations in cool environments to more efficiently use available thermal energy and provide flexibility to shift from semivoltine to univoltine cycles in warm years. At the warmest sites, excess thermal units beyond what can be used by specific life stages are acquired, suggesting that these same adaptations result in wasted thermal energy and may serve to constrain a shift to bivoltinism.

At our warmest site, CA34.2100-09 T2, a proportion of offspring from adults that attacked a tree in late June were capable of completing development by the fall of the same year, as observed previously (DeLeon et al. 1934, Reid 1962, Mitton and Ferenberg

Table 5. Mixed-model results testing the effect of tree bole aspect, sex, emergence period, and dbh on adult size of beetles that completed a generation in 1 year (univoltine only) and a comparison among univoltine and semivoltine (2 years to complete a generation) beetles at the same site.

Effect	Num, Den df	F	P
Univoltine only			
Aspect	1, 58.0	0.72	0.3986
Sex	1, 338.0	643.23	<0.0001
Aspect × sex	1, 340.5	4.33	0.0382
Emergence period	3, 39.5	3.84	0.0167
Aspect × emergence period	3, 35.5	3.67	0.0210
Sex × emergence period	3, 326.5	0.97	0.4060
Aspect × sex × emergence period	3, 329.0	0.99	0.3981
dbh	1, 58.7	4.87	0.0313
Univoltine and semivoltine			
Aspect	1, 19.6	18.07	0.0004
Sex	1, 195.5	178.50	<0.0001
Aspect × sex	1, 197.5	1.88	0.1720
Emergence period	3, 9.2	0.74	0.5540
Aspect × emergence period	3, 61.9	1.81	0.1551
Sex × emergence period	3, 191.7	0.24	0.8698
Aspect × sex × emergence period	3, 193.2	0.99	0.4008
Voltinism	1, 224.7	27.15	<0.0001
Aspect × voltinism	1, 228.9	12.57	0.0005
Sex × voltinism	1, 200.1	0.98	0.3225
Aspect × sex × voltinism	1, 198.2	0.25	0.6185
Emergence period × voltinism	3, 226.1	1.76	0.1560
Sex × emergence period × voltinism	3, 193.0	1.58	0.1952
Aspect × emergence period × voltinism	3, 227.9	1.99	0.1165
Aspect × sex × emergence period × voltinism	3, 191.5	0.39	0.7614

Eighteen sites had univoltine brood with adult size measurements, and 5 had both univoltine and semivoltine brood (see Table 2). Num, numerator; Den, denominator.

2012). Brood from these adults, however, did not complete development until the middle of the following summer, resetting the population to a univoltine life cycle, indicating that strict bivoltinism did not occur. Over the 2 sample years at the CA34.2100 site, a strictly univoltine life cycle would have produced two generations. We observed three generations in 2 years, a fractional voltinism faster than univoltinism, but not bivoltinism. Few trees were attacked at this site, and by the end of the study we could not find any new mountain pine beetle-attacked trees, indicating that the endemic population collapsed. Although many factors can influence a population collapse, our results suggest that thermal regimes resulting in fractional voltinism may not be conducive to mountain pine beetle population growth. Moreover, at CA34.2100-09 T5, accumulated thermal heat during the univoltine generation was almost 4 times that at the coolest site, CA39.2920-10, where a mostly semivoltine life cycle occurred (Figure 4B). Clearly there must be traits that constrain a decrease in generation time despite more than ample thermal input.

One trait that may serve as a barrier to bivoltinism is sensitivity to cold in the egg stage (Reid and Gates 1970), minimizing the probability that eggs laid in late fall will survive winter. A second trait is a high threshold for development in the 4th instar (>15° C) that serves to synchronize cohorts and minimize the chance of the cold-sensitive pupal stage being present during winter (Bentz et al. 1991). A development threshold of >15° C would preclude completion of development during spring when temperatures are cool. Therefore, although mountain pine beetle may complete a generation in a single summer in warm years, completion of a second generation

between fall and spring is highly unlikely, particularly at cool sites and high elevations. Contrary to the speculation that climate warming will result in bivoltine populations at 3,000 m in Colorado (Mitton and Ferenberg 2012), our data indicate that bivoltinism within the realized distribution of mountain pine beetle (i.e., where it is currently found) and under current temperature conditions is highly improbable, given current adaptations. The potential for bivoltinism with climate change is a serious threat for warm pine ecosystems outside the current latitudinal and elevational range of this insect. Additional research is needed to better understand potential adaptation, beyond existing trait plasticity, that would allow a change in current developmental thresholds and rates or areas where climate change-induced increases in temperature would provide the temperature regime necessary for bivoltinism.

Females were significantly larger than males at all sites, confirming the consistent sexual size dimorphism in this species (Amman and Cole 1983, Bracewell et al. 2013). Similar to results from British Columbia (Graf et al. 2012), large trees produced the largest univoltine mountain pine beetles. dbh did not influence the size of semivoltine beetles, however, and semivoltine beetles tended to be smaller than univoltine beetles at the same site, particularly on the south side of trees. Increased time to complete a generation, combined with variable thermal conditions, could result in a tradeoff in growth and size. Because larger adults can result in greater egg size and number (McGhehey 1971), small semivoltine beetles may be less fit. In the closely related spruce beetle (*Dendroctonus rufipennis* Kirby), however, reproductive capacity of semivoltine adults did not differ from that of univoltine beetles (Hansen and Bentz 2003).

We also found that semivoltine beetles emerged earlier in the season than univoltine beetles and at cooler temperatures. Although life stage presence under the bark was not sampled, earlier seasonal emergence for semivoltine beetles suggests that some proportion of individuals may have developed to the adult stage before the second winter and only needed a temperature cue for emergence, which was slightly cooler than required for univoltine beetles. In contrast, most univoltine beetles overwinter as larvae (Bentz et al. 1991) and thereby require thermal units for continued development to the adult stage, in addition to an adult emergence temperature cue. Although median emergence timing of semivoltine beetles was on average 35 days earlier than that of univoltine beetles, it was never earlier than the first part of July during our sample years, and there was considerable overlap between univoltine and semivoltine emergence, suggesting that geneflow occurs between the cohorts. These results also suggest that summer emergence timing of semivoltine beetles may not be as asynchronous and deleterious for a population as previously thought (Logan and Bentz 1999, Safranyik and Carroll 2006), especially as the proportion of univoltine beetles increases. Several high-elevation locations with a mix of univoltine and semivoltine brood were in the outbreak phase, indicating that a strict univoltine life cycle may not be necessary for substantial levels of tree mortality to occur.

Male and female adults that emerged later in the season were generally smaller than adults emerging early, also supporting previous findings (Safranyik and Jahren 1970, Bentz et al. 2001, Graf et al. 2012). These differences were most pronounced on the south bole aspect. Although faster development on the warmer south bole aspects could result in small adult size, we did not find that adults emerged earlier from south relative to north bole aspects. Instead, larval development of eggs oviposited later may be in a more competitive and less nutritious growing environment (Graf et al. 2012),
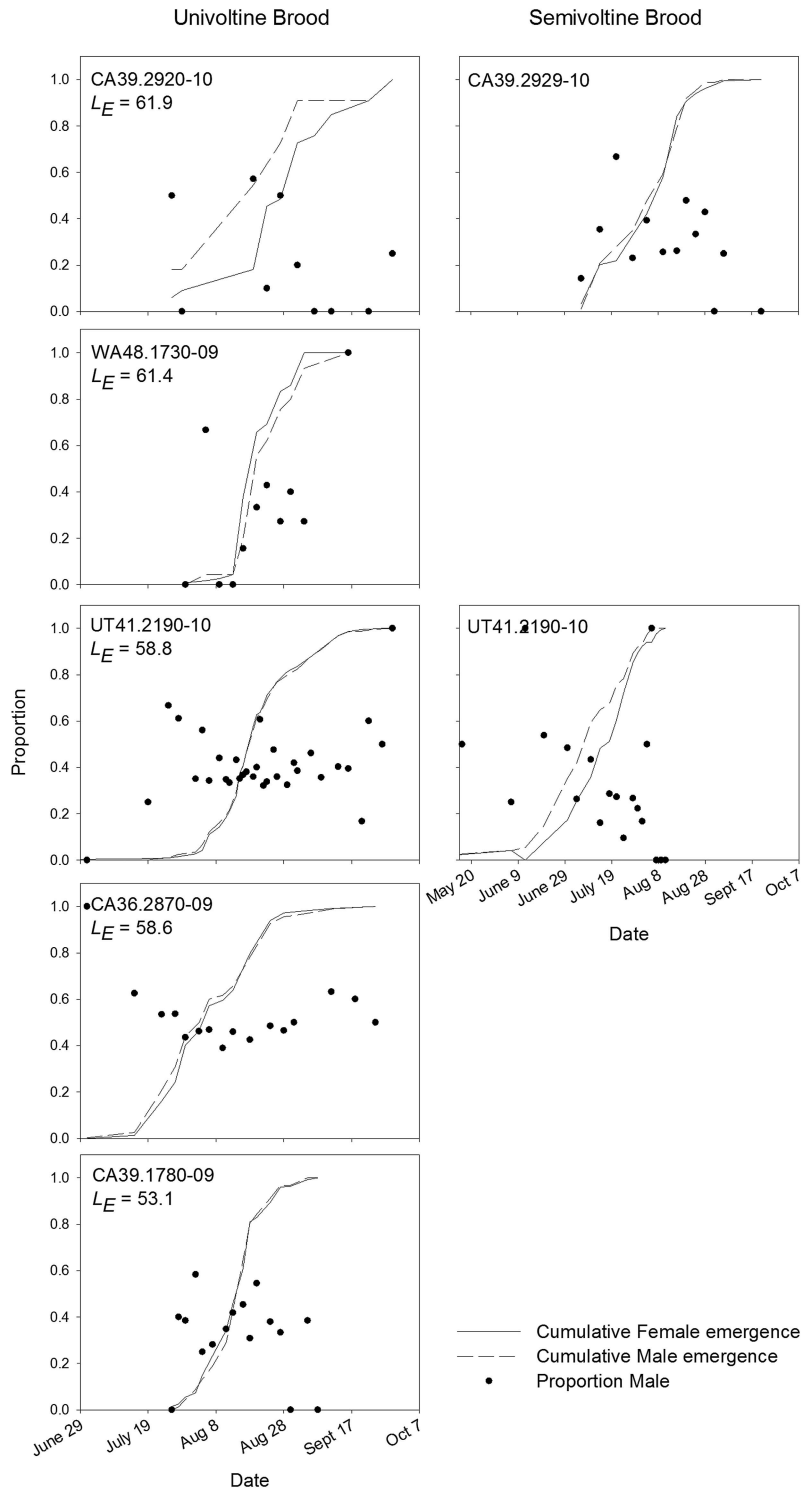
Figure 7. Proportion of brood emerged by date that were male and the cumulative proportion of female and male emergence at 5 sites across a range of latitude and elevation. Sites are arranged with the most northern location at the top. The left column shows brood that developed on a univoltine life cycle, and the right column shows brood that developed on a semivoltine life cycle. (See Table 1 for site information.)

particularly on the south side. South bole aspect habitats are more variable and stressful because of direct solar radiation and increased seasonal temperature fluctuations relative to north aspects, potentially contributing to small adult size. Smaller adults tend to have fewer lipids (Graf et al. 2012) and reduced reproductive capacity (McGhehey 1971, Elkin and Reid 2005).

Adult size and development time are both consequences of growth and developmental processes, can both influence fitness components, and are often strongly correlated. Long development time at low temperatures is predicted to result in large adult size and fast development at high temperatures in small adult size, although there can be significant fitness tradeoffs that complicate these simple

pathways (Kingsolver and Huey 2008). In laboratory studies, mountain pine beetles tend to be smaller when reared at higher temperatures (Amman and Cole 1983, Safranyik and Whitney 1985, Bentz et al. 2011). In our field study, however, adult size was not correlated with L_E, a proxy for latitude and elevation of a site (Figure 6). Instead, the largest individuals were found at sites with host trees other than lodgepole pine, including single-leaf pinyon pine, sugar pine (*Pinus lambertiana* Dougl.), limber pine (*Pinus flexilis* James), whitebark pine, and western white pine. When several host tree species were monitored at the same site, we also found that beetles emerged from western white or whitebark pine were significantly larger than beetles that developed in lodgepole pine at that same site. At these sites, dbh was not significant in explaining differences among different host tree species. Therefore, although we did not measure phloem thickness, which can significantly influence adult size and in some studies is correlated with dbh (Amman and Cole 1983, but see Graf et al. 2012), the fact that dbh was not significant suggests that the differences are not entirely due to phloem thickness. Nutritional differences among tree species may also be important. Further research is needed to elucidate the role of host tree species in mountain pine beetle fitness.

Increased beetle fitness in five-needle pine host trees has been observed previously. Langor (1989) found that mountain pine beetle infesting limber pine had significantly higher fecundity and higher survival than beetles infesting lodgepole pine. Greater brood production in five-needle pines was also observed in the laboratory (Amman 1982) and field (Dooley 2012). The CA36.2870-09 and −10 sites, where mountain pine beetle only infested limber pine, was a relatively warm, univoltine site that produced the largest beetles and the highest proportion of males. Larger beetles have more lipids (Graf et al. 2012), which can positively influence dispersal (Jactel 1993) and reproductive capacity (McGhehey 1971, Elkin and Reid 2005). The higher proportion of males at the CA36.2870 site may also be an indicator of a favorable environment, because male mountain pine beetle are suspected to be more vulnerable to stressful conditions (Amman and Pace 1976). Warming temperatures associated with climate change that allow some proportion of brood at high elevations to shift from semivoltine to univoltine, compounded by the potential nutritional benefits of five-needle pines, undoubtedly has contributed to recent mountain pine beetle-caused mortality in high-elevation ecosystems (Macfarlane et al. 2013). Reduced cold-induced beetle mortality during years with warm winters has also played a role, not only in high elevation ecosystems but also in lodgepole pine-dominated areas (Preisler et al. 2012, Sambaraju et al. 2012).

An exception in species-related adult size was at the UT41.2190 site where adult size was among the largest, although the host tree species was lodgepole pine. Bracewell et al. (2013) also found that mountain pine beetles from lodgepole pine near the UT41.2190 site were larger than beetles from lodgepole pine at a similar latitude in California. Differences in size between Utah and California beetles infesting lodgepole pine probably contributed to mountain pine beetle being originally described as two separate species. Beetles from the east side of the Great Basin were generally larger than those found on the west side (Wood 1982). Although the two species were synonymized to *D. ponderosae* based on morphology (Wood 1963), recent evidence suggests significant reproductive isolation in mountain pine beetle on either side of the Great Basin, which could represent the early stages of speciation (Bracewell et al. 2010).

In laboratory studies, the proportion of *Ips typographus* (Linnaeus) males declined at the highest rearing temperatures (Wermelinger and Seifert 1999). Temperature has also been found to affect sex ratio in some insect populations by causing a transformation of males into females at high temperatures (Saccone et al. 2002, Sanchez 2008). In our field study, sex ratio varied among the sites, and there was a trend for fewer males to be found at the coolest sites with semivoltine brood and at sites with the lowest emergence. These results suggest that males may have been influenced by unfavorable conditions, although not necessarily high temperatures. We found no significant differences among emergence periods in sex ratio, contrary to the results of Rasmussen (1980). Within a population, male mountain pine beetle were always smaller than female mountain pine beetle although there was not a consistent pattern for either males or females to emerge first. Bentz et al. (2011) also observed that females attain a larger size than males within a similar development time, suggesting differential allocation of energy to fitness characters between the sexes.

Conclusions

Our study is the first field-based report of mountain pine beetle life cycle timing and associated life history traits in a considerable range in elevation and latitude across the western United States. With the exception of a very cool and very warm site, the number of days required to complete a generation was surprisingly similar. The thermal units accumulated during a generation, however, differed greatly among sites and was significantly less at the coolest sites. This pattern can be explained by evolved adaptations including developmental rates and thresholds that serve to synchronize cohorts and minimize the presence of cold-sensitive life stages in winter. These same adaptations reduce the capacity of mountain pine beetle at the warmest sites to take full advantage of increased thermal units. Our results suggest that mountain pine beetle has evolved in cool rather than warm environments and that considerable warming may be required to cross the physiological barrier to bivoltinism. If this occurs, however, expansion of mountain pine beetle into warm pine ecosystems in the southern United States and Mexico is a possibility, and research is needed to evaluate thermal regimes that would facilitate a southern range expansion.

Accumulated temperature at a site was not a major driver of adult size or sex ratio. Instead, adult size was greatest at sites with host tree species other than lodgepole pine. Therefore, although lodgepole pine is the most widely available pine host across the range of mountain pine beetle, it may not necessarily produce offspring with the greatest fitness advantage, relative to those of other host tree species. Warm winter temperatures relax cold temperatures that can cause significant mortality in mountain pine beetle and warm summer temperatures facilitate univoltinism in at least some brood in high-elevation ecosystems. Both have enabled increased population success at the northern edge of the distribution and at higher elevations (Cudmore et al. 2010, Safranyik et al. 2010, Macfarlane et al. 2013, Sambaraju et al. 2012). Mountain pine beetle populations with the capacity to immediately take advantage of added thermal units in a warming climate are those in marginally cool habitats, often infesting host tree species that are at risk of decline in a changing climate. Our results provide important baseline information on thermal requirements for mountain pine beetle voltinism pathways across forested habitats in the western United States. This information, in addition to an understanding of the potential for adaptation, will be valuable in evaluating mountain pine beetle response to continued

climate change and can be used to inform management strategies for host tree conservation of important at-risk species in environments that are dramatically changing.

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