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Western pine beetle voltinism in a changing California climate

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Abstract

1. Recent hot droughts in California resulted in ponderosa pine (*Pinus ponderosa*) mortality attributed to drought and western pine beetle (WPB, *Dendroctonus brevicomis*). While drought alone can cause tree death, direct warming effects on WPB are a contributing factor. Research on WPB generation timing (voltinism), however, is lacking.
2. We monitored WPB tree attacks and adult emergence timing at two California sites and developed a degree-day model from field-observed data. Historical, contemporary, and future temperatures for several California sites were used with the model to examine trends in WPB voltinism.
3. Field data showed a single summer and an overwinter generation at a northern California site. As summer temperatures increased beyond 1900–1980 averages, the predicted number of full and partial WPB generations by 2021 had increased from ~2 annual (one summer and one overwinter) generations historically to ~2.3 at two northern California sites and from ~2.3 to ~3.2 at two warmer California sites.
4. Historical and contemporary data suggest winter warming was not sufficient for an additional generation overwinter. Instead, increases in generations were driven by summer and fall temperatures.
5. Unconstrained increases in the number of future annual generations will be limited by complex, but not well understood, WPB thermal adaptations. Increased knowledge of temperature-driven WPB population growth will improve forest vegetation models aimed at predicting ponderosa pine mortality in a changing climate.

KEYWORDS
bark beetle, climate change, *Dendroctonus brevicomis*, drought, voltinism

INTRODUCTION

A combination of decreasing precipitation and increasing temperature has been associated with tree mortality globally in recent decades (Allen et al., 2015; Brodribb et al., 2020). In the western United States (US), conifers across multiple elevations and latitudes have been affected by these 'hot droughts' (Bentz, Millar, et al., 2022; Breshears et al., 2005; Fettig et al., 2019; Millar & Stephenson, 2015), foretelling future tree mortality as the climate driving these events amplifies. Predicting climate change effects on tree mortality is complex, however, as both direct and indirect dynamics play a role. Physiological processes that can result in direct tree mortality include water limitation that results in hydraulic failure through stomatal closure and subsequent carbon starvation, and extreme temperatures that cause vapour

† Retired.

pressure deficits leading to xylem cavitation and loss of water transport (Adams et al., 2017; Hartmann et al., 2018). Carbon starvation can also have a negative effect on quantitative and qualitative resin defences that are used against bark beetle attacks (Anderegg et al., 2015; Kolb et al., 2019; McDowell et al., 2008). Importantly, warming temperatures associated with recent drought can directly influence native bark beetles (Coleoptera: Curculionidae, Scolytinae) and their capacity for increased population growth (Bentz et al., 2014; Buotte et al., 2017; Weed et al., 2015).

A recent hot drought in the central and southern Sierra Nevada, California, estimated to be the most severe in the last 1000 years (Griffin & Anchukaitis, 2014; Robeson, 2015), resulted in the death of an estimated >100 million trees due to a combination of drought-related stress, dense stands, and bark beetle attacks (Fettig et al., 2019; Koontz et al., 2021; Stephenson et al., 2019; Young et al., 2017). Most of the bark beetle-caused tree mortality during this event was due to the western pine beetle (WPB *Dendroctonus brevicomis* LeConte), a native bark beetle of western North America that attacks and reproduces in live ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) and Coulter pine (*Pinus coulteri* D. Don) (Miller & Keen, 1960). Historically, WPB outbreaks have been recorded throughout the range of ponderosa and Coulter pine in California since the early 1900s, including the hot and dry 'dust bowl' years in the early 1930s (Miller & Keen, 1960). Recent outbreaks in southern California (2001–2004) and the south Sierra Nevada (2015–2017) were also associated with drought events (California Forest Pest Council, 2003; Fettig, 2019; Koontz et al., 2021). While water stress plays a large role in ponderosa pine susceptibility to WPB, the warm temperatures associated with recent droughts also likely contribute through direct effects to WPB population growth.

WPB development and survival are driven in part by temperature, and warming at appropriate times of the year could positively affect population growth (Deutsch et al., 2008; Logan & Bentz, 1999). Relative to other bark beetle species native to the United States (Bentz, Hansen, et al., 2022; Bentz & Jönsson, 2015), little research has been conducted on temperature-dependent phenology of WPB. Miller and Keen (1960) summarized WPB generation timing, based on adult emergence from infested trees, using data collected in multiple field studies during the early 1900s. In northern California and at higher elevations, two WPB generations were observed; tree attacks in early June resulted in one summer generation, with an overwinter generation resulting from attacks in late August. In southern California and lower elevations, attacks in March were observed, resulting in two summer generations in addition to the overwinter generation (Miller & Keen, 1960). The authors noted that an increase or decrease by a single summer generation can occur with interannual variation in temperature. Moreover, a partial generation can occur wherein some proportion of new adults from a summer generation emerge in the fall, while the remainder overwinter and emerge the following year. In a recent modelling study based on data in Miller and Keen (1960) and other sources, simulations suggest that a partial generation (i.e., less than 100% adult emergence from a late summer/fall cohort) could increase ponderosa pine mortality during a hot drought when trees are stressed (Robbins et al., 2022).

Predicting forest dynamics in a changing climate is complex, and quantitative descriptions of the influence of temperature on bark beetles that can cause landscape-scale tree mortality are critical for projections of ecosystem responses to climate change (Anderegg et al., 2015; Hartmann et al., 2018). Appropriate data for model development, however, are only available for a few species (Bentz & Jönsson, 2015). To predict future WPB response to changing climatic conditions, information is needed on thermal requirements for brood development and generation timing (voltinism). Following oviposition, WPB develops through four larval instars, prepupa, and pupa, prior to becoming an adult. All lifestages occur beneath the bark other than during adult dispersal. Although lifestage-specific investigations have not been conducted for WPB, it appears to have a relatively high-temperature threshold for development from a prepupa to pupae (~12–15°C) (Miller & Keen, 1960), similar to the threshold for prepupal diapause found in mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Bentz & Hansen, 2018) and spruce beetle (*D. rufipennis* Kirby) (Hansen et al., 2011). In mountain pine beetle, this physiological trait prevents development to the cold-intolerant pupa stage (Bleiker & Smith, 2019) before the onset of winter (Bentz et al., 2014; Soderberg et al., 2021). Although WPB is multivoltine and mountain pine beetle is generally univoltine (Bentz & Powell, 2014), this trait, either a threshold or diapause, would likely force any increase in the number of WPB generations per year to occur during summer. Although the timing of WPB attack and emergence can vary among years (Miller & Keen, 1960), field data describing the number of generations currently occurring in California pine forests has not been described. Moreover, how generation timing and the number of generations may change in a future climate has not been investigated.

Our overall goal was to describe contemporary WPB generation timing in relation to air temperature at two sites representing two latitudes within the Sierra Nevada and Cascade, California mountain ranges. These data provide a new baseline for evaluating potential future population responses to changing climate. Using the field-collected data, we also parameterized and evaluated a degree-day model for predicting the number of WPB summer generations. The model was then used to examine historical and potential future changes in the number of annual WPB generations at four representative ponderosa pine sites in California, including two sites with historical written accounts of WPB lifecycle timing (Miller & Keen, 1960).

METHODS

Study sites, WPB attack, and emergence data

Study sites on the Lassen and Stanislaus National Forests (Figure 1, Table 1) were identified based on having elevated levels of WPB-caused ponderosa pine mortality and ease of access to facilitate frequent monitoring and beetle collection visits. These locations were also selected to incorporate population data from two latitudes within the range of WPB in California. The Lassen data were used for model parameterization and

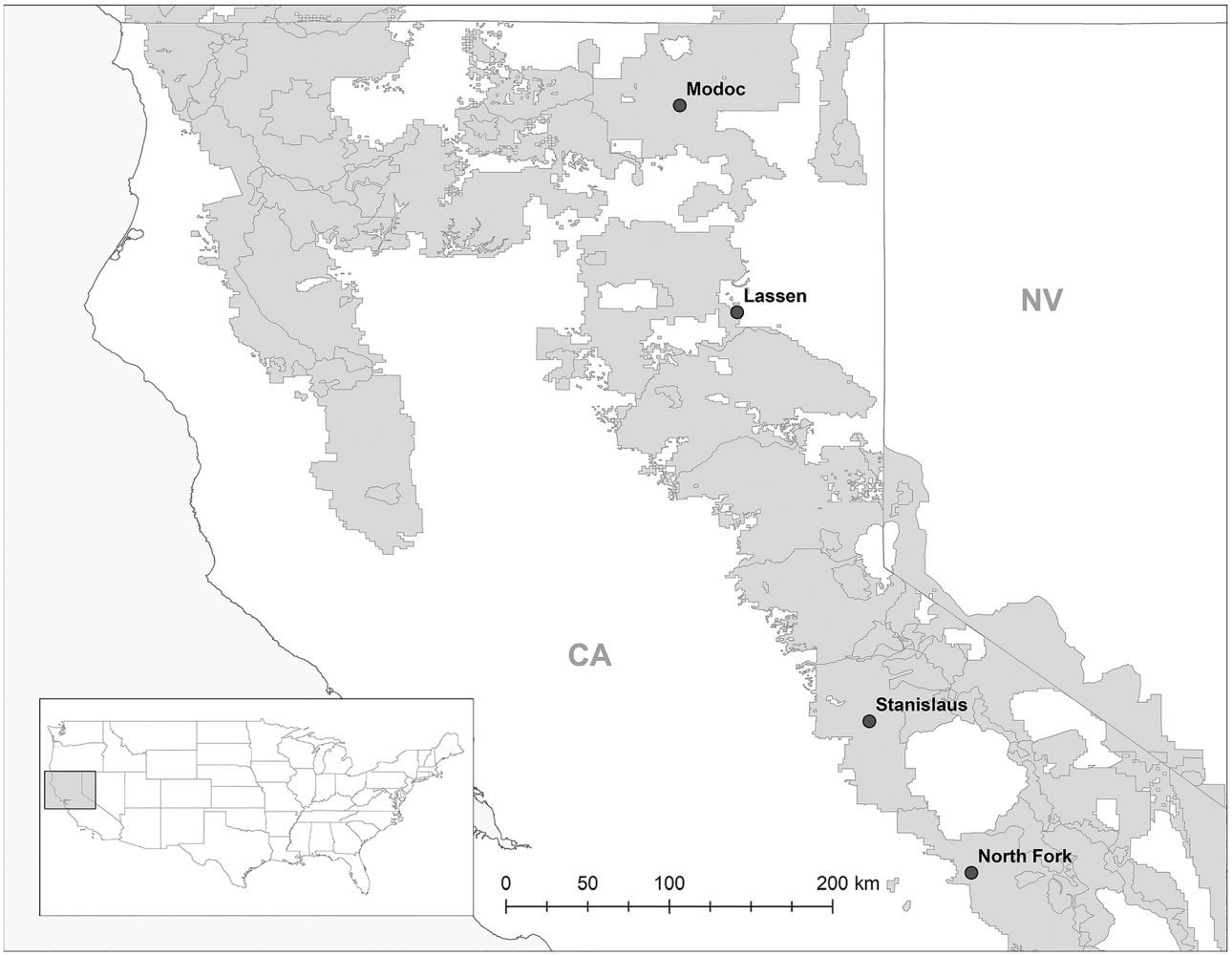

FIGURE 1 Study sites within USDA National Forest boundaries in California used for monitoring and modelling western pine beetle generation timing and voltinism. Field data were collected at the Lassen and Stanislaus sites (Table 1), and Modoc and North Fork sites have historic descriptions of western pine beetle activity (Miller & Keen, 1960). Historic, contemporary, and future projected temperatures from all sites were used to evaluate western pine beetle voltinism trends.

TABLE 1 Location information for California sites used in analyses.

Site name	National forest	Latitude	Longitude	Elevation (m)
Modoc	Modoc	41.543	−121.126	1470
Lassen	Lassen	40.4029	−120.8097	1518
Stanislaus	Stanislaus	38.1503	−120.0811	1628
North Fork	Sierra	37.3156	−119.518	1300

Note: Field data were collected at the Lassen and Stanislaus sites, and North Fork and Modoc are two sites with historical western pine beetle activity described in Miller and Keen (1960).

Stanislaus data for model evaluation. Hourly air temperatures were monitored at each site by placing a shielded temperature probe (Onset Computer Corporation, Bourne, MA) on the north side of a tree at 2.0 m above ground. Temperatures were monitored year-round at the Lassen site, and from spring through fall at the Stanislaus site.

The WPB population at the Lassen site was at an endemic to incipient population phase based on the number of tree mortality groups and prior year infestation levels (see Egan et al., 2016). Five individual ponderosa pines (32.97 ± 4.1 cm dbh, diameter at breast height) were baited with aggregation lures (*exo*-brevicomin and frontalin; Synergy Semiochemical Corporation, Burnaby, BC, Canada) on 19 May 2017, just prior to predicted WPB flight based on local weather conditions, prior observations, and past research (Miller & Keen, 1960). Attacks were monitored weekly around the bole circumference from 0.3 to 1.5 m above ground line until attacks diminished and bole colonization appeared complete. Individual attacks were marked with different coloured push pins each visit. At the end of the attack period, two 30 X 60 cm nylon mesh screen emergence cages were stapled to the bole, one each on the north and south-facing sides of the bole and centred at a height of 1.4 m (Figure 2). Each cage was fitted with a small centrifuge tube at the base for collecting adult beetles. When adult emergence from infested trees began, new trees within 200 m of the original

FIGURE 2 Coloured push pins denoting week of attack were used to monitor the timing of western pine beetle attacks (left), and tree cages were used to quantify adult emergence timing from infested trees (right). Photo credit D. R. Cluck.

trees were baited. This process was repeated for a potential second summer generation by baiting five new ponderosa pine (38.35 ± 5.6 dbh) on 4 August 2017, and a potential third generation by baiting three new trees (34.54 ± 4.8 dbh) on 21 September 2017. Adults were collected weekly from each caged tree until emergence was complete. Collection tubes remained on cages during the winter but were not checked for adult beetles until the following spring. Three new trees (25.91 ± 4.1 dbh) were baited on 26 April 2018, three additional trees (35.1 ± 8.9 dbh) were baited on 22 July 2018, and a third set of three trees (34.6 ± 4.8 dbh) were baited 18 September 2018. Emergence from each tree was monitored as described above.

The WPB population at the Stanislaus site was considered in the post-epidemic population phase. Temperature data collection, tree baiting, attack monitoring, and beetle collections from emergence cages were conducted in the same manner as described for the Lassen site except that attack monitoring and collection of adult beetles occurred less frequently. Three ponderosa pine (67.3 ± 4.1 dbh) were baited on 2 May 2017, and three additional trees (51.4 ± 1.5 dbh) were baited 2 August 2017. In 2018, three trees (43.8 ± 9.1 dbh) were baited 1 April, and an additional three trees (38.7 ± 8.6 dbh) were baited on 28 June. Trees attacked in late summer of 2017 or 2018 were not monitored for emergence the following summer and no trees were monitored in 2019.

At both sites, the cumulative proportion of attacks for each sample date and tree was calculated as the total attacks to that date divided by the total attacks on the tree. Cumulative attacks were calculated separately for each attack period. Cumulative proportion emergence was calculated similarly for each tree, sampling date, and emergence period.

Degree-day models

Degree-day calculations

Hourly temperature recordings were initiated on 19 May 2017 at both sites and ended on 20 June 2019 at Lassen and 4 March 2018 at Stanislaus. To calculate degree-days with a 1 January biofix for each year, missing daily maximum and minimum temperatures from 1 January to 18 May 2017 were estimated for both sites. Parameters to estimate missing data were derived from a linear regression with observed daily data and data from nearby NOAA (https://www.ncei.noaa.gov/cdo-web/) and RAWS (https://raws.nifc.gov/) monitoring stations. For these days, hourly values were then calculated from the predicted daily maximum and minimum temperatures based on a sine-wave function. Observed hourly temperatures recorded at each site were used for degree-day calculations for the remainder of each year.

Due to a potential high-temperature threshold for prepupal development that could limit brood development in winter (Bentz & Powell, 2014; Miller & Keen, 1960), we hypothesized that changes in the number of generations per year at our sites would occur during summer. Because we only had field observations for one complete summer generation, we modelled the degree-days required for completion of a single summer generation based on timing of spring attacks and subsequent adult emergence of the first generation. Then, the number of additional summer generations was calculated based on the degree-days required for the first generation and the remaining degree-days in the year (see below). Degree-days for first attacks in spring (i.e., following emergence of the overwinter generation) and degree-days required for completion of a summer generation were therefore calculated separately. To predict the first set of attacks at each site, degrees days-were calculated beginning January 1 in 2017 and 2018. Degree-days were then accumulated and summed from 1 January to each sample day attacks were observed (spring attack period). Because attacks and emergence timing differed among the trees at a site, degree-days required for a summer generation were calculated separately for each tree. Degree-days were summed from the day that attacks were first observed to each sample day that emergence was recorded, by tree and site.

We hypothesized that optimal base temperatures for degree-day calculations would differ for predicting spring attacks and the completion of a summer generation. Spring attacks follow emergence of the overwinter generation that begins with attacks the previous summer. Because of this, the oldest lifestages (i.e., instar 4, prepupae, pupae) would likely be present from 1 January to late spring/early summer emergence, and a required developmental threshold between ~12 and 15°C was suggested (Miller & Keen, 1960). By contrast, development through all lifestages would occur during a summer generation, and a low temperature development threshold for all lifestages would be more descriptive. Low and upper-temperature thresholds, however, have not been investigated for any WPB lifestage. We analysed our data to capture the range of potential low and upper-temperature thresholds for development of the overwinter generation, with subsequent attacks on trees, and development of a summer generation. Degree-days were calculated using a series of low threshold temperatures (LTT) between 3° and 15°C and upper threshold temperatures (UTT) between 30° and 35°C using hourly temperatures and trapezoidal numerical integration (Matlab 2022a, trapz function). Potential UTT temperatures were based on reported values for *D. ponderosae* (McManis et al., 2018) and *D. frontalis* (Wagner et al., 1984).

Model development and evaluation

We observed WPB attack and emergence timing at two sites. Because sampling at the Lassen site was more frequent than at the Stanislaus site, we used Lassen data for degree-day model development and data from the Stanislaus site were reserved for model evaluation. As described above, we fit separately the first set of attacks in early summer and emergence of that summer generation. Data from 2017 and 2018 were pooled for model development. We used the cumulative Weibull distribution (minpack.lm package, nlsLM function) (Elzhov et al., 2016) (R Core Team, 2022) to predict the observed cumulative degree-days (cumDD) required for an observed cumulative proportion of attacks following emergence of the overwinter generation (*A. cumprop*) and emergence of a summer generation (*E. cumprop*):

$$A.cumprop = 1 - e^{-\left(\frac{cumDD}{b}\right)^{a}} \quad (1)$$

$$E.cumprop = 1 - e^{-\left(\frac{cumDD}{d}\right)^{c}} \quad (2)$$

where *a*, *b*, *c*, and *d* are estimated parameters.

Each model was fit using degree-days calculated from a series of LTT temperatures (3°C, 5°C, 7°C, 9°C, 10°C, 13°C, and 15°C) and UTT temperatures (30°C, 32°C, and 35°C). The residual standard error from Weibull model fits was used to determine the most descriptive LTT and UTT temperature thresholds for accumulating degree-days to predict attacks from an overwinter generation (*A. cumprop*) and development of a summer generation (*E. cumprop*). The cumDD required for a given proportion (*p*) of *A. cumprop* and *E. cumprop* was determined by taking the inverse of *Equations 1* and *2*, using the estimated parameters for each:

$$A.cumDD = b * (-\log(1-p))^{1/a} \quad (3)$$

$$E.cumDD = d * (-\log(1-p))^{1/c} \quad (4)$$

The calendar date for *p* attacks or *p* emergence was assigned as the dates when the calculated *A.cumDD* or *E.cumDD* occurred in the temperature record. For example, to predict the cumDD and date of median attacks or emergence, *p* was set to 0.5.

Predicting the number of summer generations at a site was accomplished through the following steps: (1) predict the distribution of attacks following an overwinter generation using DDs accumulated from 1 January and estimated parameters for *A. cumDD*; (2) accumulate DDs from the first attack to predict adult emergence of the first summer generation using estimated parameters for *E.cumDD*; (3) accumulate remaining DDs for predicting adult emergence for a second summer generation using estimated parameters for *E. cumDD*; (4) repeat step 3 to test for additional summer generations. The number of a full and partial summer generation for a given site and year of temperatures from 1 January to 31 December was output. We also checked the cumDDs based on Equation (2) beginning 1 November to the earliest first attack date in spring the following year to evaluate if there were sufficient cumDDs for a partial generation to complete an additional generation over winter.

We compared output from the combined model with the Lassen site data used for model development, in addition to the independent Stanislaus site data. Linear regression (lm function, R Core Team, 2022) was used to compare observed cumulative proportion and model predictions by year and type (i.e., attacks following the overwinter generation or first summer emergence). A full second summer emergence period was not observed either year at the Lassen site, and emergence from the overwinter generation was not monitored at the Stanislaus site.

Historical and future temperature regime simulations

In addition to our two study sites, we selected two CA locations with historical records of WPB activity and were also near our study sites (Miller & Keen, 1960). These sites were used to investigate historic and future trends in WPB voltinism. Historic and future projected temperatures at each site were modelled using BioSIM 11 (Régnière et al., 2017). BioSIM generates site-level daily maximum and minimum temperatures based on nearby weather stations, adjusting for latitude, elevation, and topography. Hourly temperatures were estimated from daily maximum and minimum temperatures based on a sinewave function and degree-days were then estimated based on numerical trapezoidal integration as described above. Simulated future daily normals were generated in BioSIM using the delta method and climate projections from the CMIP6 scenario and global climate models (GCM) ACCESS-ESM1.5, CanESM5.0.3, MRI-ESM2.0, GFDL-ESM4, and UK-ESM1-0-LL (Fortin et al., 2022). We used projections under the most aggressive scenario in assumed fossil fuel use, representative concentration pathway (RCP) 8.5 (Schwalm et al., 2020). The WPB degree-day model was run using annual modelled historical records from 1900 to 2021 for each site. The model was also run for each location using projected daily temperatures averaged across the five GCMs for future climate normals periods (2041–2070, 2071–2100).

RESULTS

Observed WPB attacks and emergence

At the Lassen site, 2017 attacks began the first week of June on trees baited 19 May. Median attacks occurred by 23 June and >95% of attacks on all trees occurred by 21 July (Figure 3b). The first adults of the summer generation were collected from emergence cages on 31 July, and adult emergence timing varied by tree. Three trees had >95% emergence by 6 September, and two trees by 9 November, with the remaining adults emerging in 2018 including two adults that emerged on 16 July 2018, a little over a year after attack (Figure 3b). Median attacks on new trees baited 4 August occurred between 11 and 17 August (Figure 3c). A small proportion of emerged adults (~ 5% of total emergence) were collected from cages on these trees

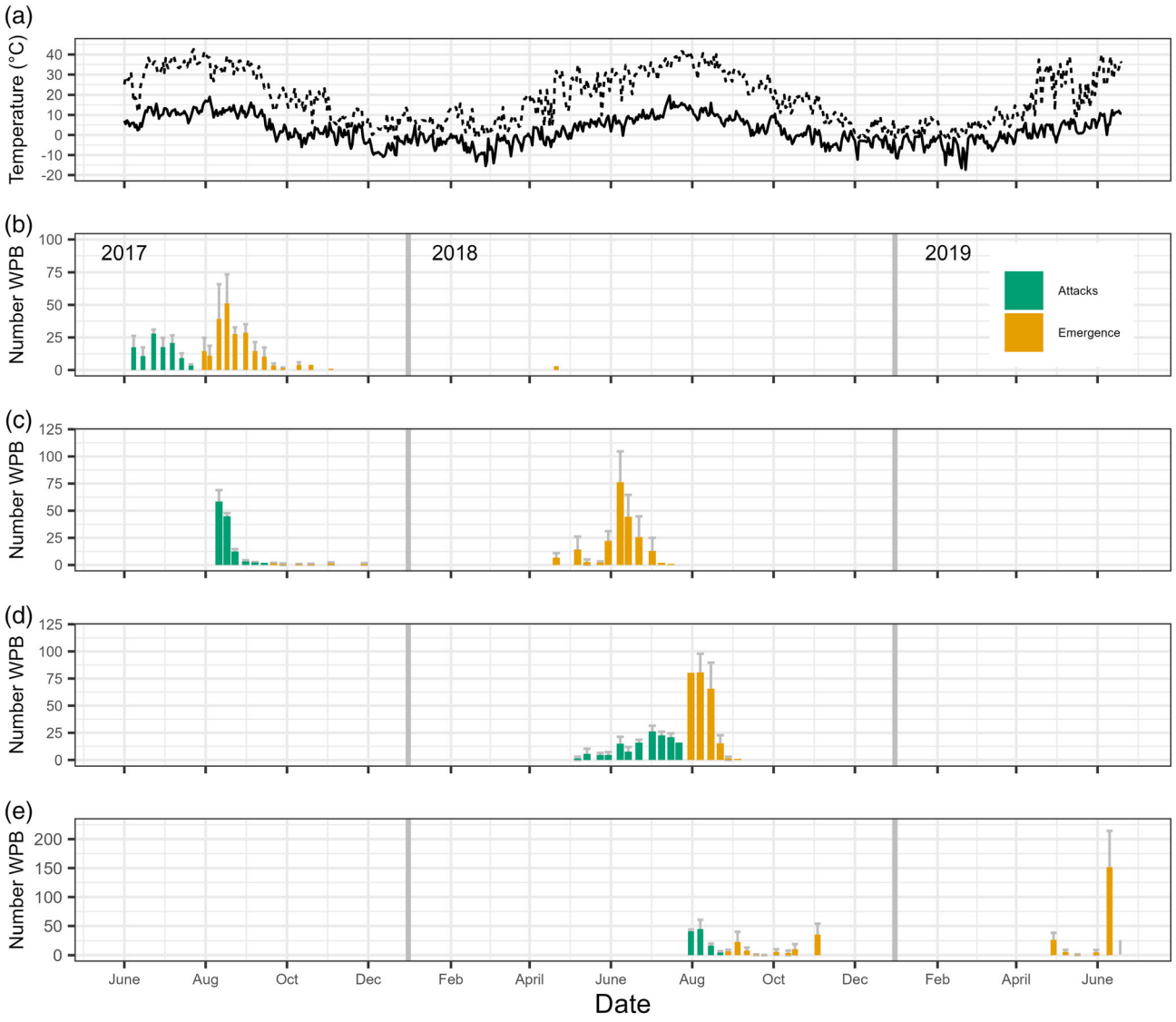

FIGURE 3 Daily maximum and minimum temperatures recorded at the Lassen site (a), number of western pine beetle (WPB) spring attacks and WPB emerged from trees during the first summer generation at the Lassen site in 2017 (b), WPB attacks following emergence of the 2017 summer generation and emergence from these trees in 2018 (c), WPB spring attacks and emergence of the summer generation in 2018 (d), and WPB attacks following emergence of the 2018 summer generation and emergence from these trees in 2018 and 2019 (e). Shown are the mean and standard error among trees.

in the fall of 2017, with the majority of emergence beginning in April 2018 (i.e., an overwinter generation) (Figure 3c). To see if new trees would be attacked during the low emergence period in the fall of 2017, three new trees were baited on 21 September 2017. Very few attacks occurred on these trees, and they were evaluated for WPB activity and phloem condition on 26 April 2018 by removing small sections of bark. One tree contained WPB larvae but only on the south face, one was colonized by secondary bark and woodboring beetles including *Ips emarginatus*, *Acanthosinus* spp. and *Monochamus* spp. and the third had a few unsuccessful WPB attacks. These results suggest that WPB adults emerging in fall 2017 were mostly unsuccessful at establishing new brood.

Of the new trees baited on 26 April 2018 at the Lassen site, only one received an emergence cage, and median attacks were observed by 22 June (Figure 3d). The two other trees could not be utilized for continued monitoring due to insufficient attack density for one tree and the presence of a yellow jacket nest at the base of the other. Two additional infested trees within the same group attack (and same attack timing) as the baited trees were caged in their place. All emergence cages were installed on 16 July with first adults collected 22 July and median emergence by 7 August 2018 (Figure 3d). Attacks on the set of trees baited on 22 July began immediately, with median attacks by 7 August (Figure 3e). A range of 14% to 39% of total adults emerged prior to 3 November 2018, and the remainder emerged the following summer, beginning 29 April 2019 (Figure 3e). A limited number of attacks occurred from 3 October to 3 November 2018 on the third set of trees baited on 18 September 2018. These trees received a few additional unsuccessful attacks in the spring of 2019, and two

were still green as of 8 July 2019. One tree showed slight crown fade but successful colonization of the lower bole by WPB was not observed. These results suggest that although there were a greater number of adults that emerged in the fall of 2018 than 2017, fall attacks we monitored at the Lassen site were unsuccessful both years. Attacks occurred earlier in the spring in 2018 compared to 2017, potentially contributing to the greater fall emergence in 2018 (Figure 3). Attack and emergence timing of WPB adults at the Stanislaus site were intermittently recorded in 2017 and 2018 and observations can be found in Figure S1.

Degree-day models

For predicting spring attacks, cumDD >13°C (LTT) and <30°C (UTT) had the lowest residual standard error when fitting the cumulative Weibull function to observed Lassen data. CumDD >5°C (LTT) and <30°C (UTT) had the lowest residual standard error when fitting the Weibull function to observed emergence of the first summer generation. Parameters for each model and estimated cumDD for 5%, 50%, and 95% spring attacks and emergence are shown in Figure 4. When predictions were compared to the data used for model development (i.e., the Lassen site), 91% (adjusted [Adj.] $R^2 = 0.91$, $F_{1,60} = 614$) of the variation was explained for spring attacks, and 90% (Adj. $R^2 = 0.9044$, $F_{1,47} = 454.9$) for predicting the first summer generation. The combined model (*A. cumDD* and *E. cumDD*), which predicts emergence of the first summer generation based on predicted attacks, explained 72% (Adj. $R^2 = 0.716$, $F_{1,36} = 94.4$) of the variation in the first summer generation emergence period in 2017 and 74% (Adj. $R^2 = 0.743$, $F_{1,16} = 50$) for 2018 observations. At the independent Stanislaus site, the combined model explained 82% (Adj. $R^2 = 0.818$, $F_{1,13} = 64$) of the variation in the first summer generation emergence in 2017 and 70% (Adj. $R^2 = 0.704$, $F_{1,14} = 20$) in 2018. Using recorded temperatures at each site, the combined model predicted a single summer generation at the Lassen site both years, with <30% emerging for a partial second summer generation, as observed in the field data. Also corresponding to field observations, spring attacks were predicted to occur earlier in 2018 than 2017. At the warmer Stanislaus site, one summer generation plus >91% emergence of a partial second summer generation was predicted both years. Field observations for the second summer generation at the Stanislaus site were not available for comparison.

Historical and future temperature regime simulations

Annual predictions using modelled historical data showed variability across the sites in the annual number of full and partial summer generations, with the lowest elevation and latitude site, North Fork, having the overall greatest variability among years (Figure 5). Simulations suggest there was a general increase in emergence for a partial generation occurring during the warm and dry years of the late 1920s and early 1930s when summer temperatures were warmer than historical averages at all sites except Modoc. A general trend of summer temperatures that were warmer than the historical (1900–1980) average began in ~1999 at all sites, and the warming was associated with multi-year recorded droughts in 2007–2009 and 2012–2015 (Pu et al., 2022) (Figure 5). Warming that began in ~1999 was associated

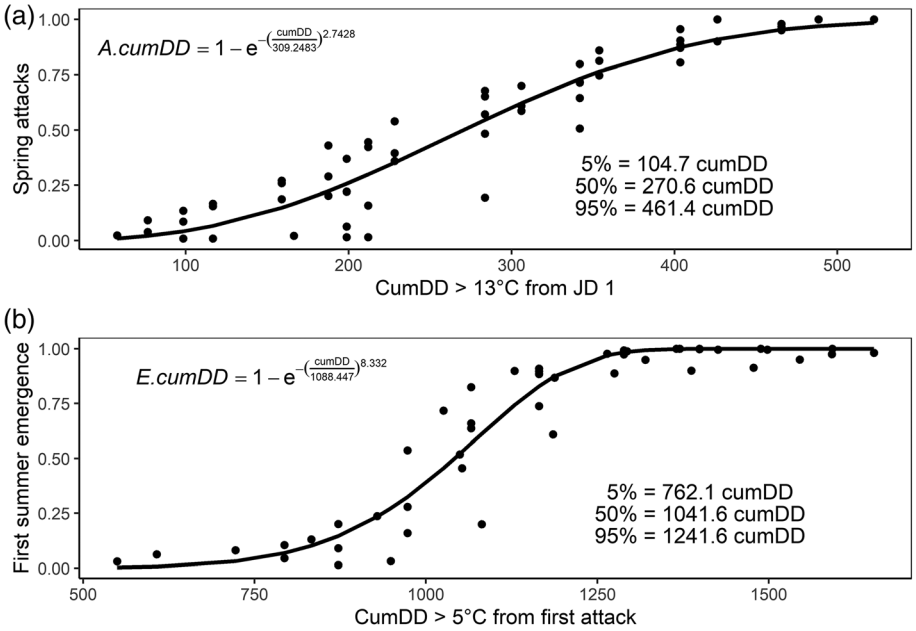

FIGURE 4 Observed and predicted (a) spring attacks (*A. cumDD*) and (b) first summer emergence (*E. cumDD*) using observed data from the Lassen site. Parameters were estimated using a Weibull function. The biofix of accumulating degree days (cumDD) for spring attacks was January 1 with a lower threshold temperature of 13°C and upper threshold 30°C. The biofix for cumDD for a summer generation was the date when 0.08 spring attacks had occurred, and the lower threshold was 5°C and the upper threshold 30°C.

FIGURE 5 Predicted number of full and partial summer generations based on historical temperature records for each site (top panel). A Loess smooth with span = 0.1 was fit to data for each site. Anomalies (°C) in average annual summer temperature (April 1 to Sept 30th) relative to the 1900–1980 period are shown in the bottom panel. Shaded areas are recent multi-year drought events recorded in California, including 2007–2009 and 2012–2015 (Pu et al., 2022). See Table 1 for site locations.

TABLE 2 Mean annual temperatures and cumDD > 5°C after model-predicted spring attacks, summed for each site using estimated historical temperatures from BioSIM.

Historical temperatures 1900–2021						
Site	Mean annual temperature (°C) 1900–1980	cumDD >5 1900–1980 mean annual	Summer generations 1900–1980	cumDD >5 2021	cumDD >5 change from 1900–1980 to 2021	Summer generations 2021
Lassen	7.9	1466.5	1.0	2056.4	590	1.3
Modoc	7.6	1403.9	1.0	2120.0	716	1.4
North Fork	11.7	2147.6	1.5	2897.4	750	2.2
Stanislaus	9.4	1618.7	1.1	2740.4	1122	2.1

Note: Temperatures were used with the combined western pine beetle (WPB) model to predict the number of WPB summer generations for each year from 1900 to 2021, and shown are model results for the historical period (1900–1980) and 2021. Also shown is the positive change in cumDD >5°C from the historical period to 2021, driving the increase in summer generations, for each site. Total annual WPB generations is the sum of one overwinter generation and predicted summer generations.

with increases in the predicted number of WPB summer generations at the two most southern sites, North Fork and Stanislaus (Figure 5). An increasing trend in predicted number of partial summer generations at the two northern sites, Lassen and Modoc, started slightly later. By year 2021, Lassen and Modoc had lower predicted number of generations compared to the North Fork and Stanislaus sites. Differences among the sites in predicted generations is a result of differences in cumDD >5°C following predicted spring attacks. Historically, the Lassen and Modoc sites were cooler in the summer (less cumDD >5°C after spring attacks) than the North Fork and Stanislaus sites resulting in lower emergence for a partial summer generation (Table 2). As temperatures warmed in the late 1990s, the average change in cumDD >5°C between historic averages and year 2021 was also greater at the North Fork and Stanislaus sites resulting in greater emergence of a partial summer generation (Table 2). Therefore, while average summer temperature increased at all sites, the warmer the

TABLE 3 Mean annual temperatures and cumDD > 5°C after model-predicted spring attacks, summed for each site and climate normals periods 2041–2070 and 2071–2100 based on 5 GCMs and the 8.5 RCP (representative concentration pathway).

	Projected climate normal					
Site	Mean annual temperature (°C) 2041–2070	cumDD >5 2041–2070	Summer generations 2041–2070	Mean annual temperature (°C) 2071–2100	cumDD >5 2071–2100	Summer generations 2071–2100
Lassen	12.0	2231.0	1.7	14.1	2726.2	2.2
Modoc	12.6	2344.3	1.8	14.3	2657.6	2.2
North Fork	16.4	3253.9	2.9	17.3	3544.7	3.2
Stanislaus	14.3	2701.7	2.2	16.3	3206.4	2.6

Note: Projected temperatures were used with the combined western pine beetle (WPB) model to predict the number of WPB summer generations for each climate normal period. Total annual WPB generations are the sum of one overwinter generation and predicted summer generations.

site the greater increase in emergence of a partial summer generation. Notably, the predicted number of full and partial summer generations in years 2014 and 2021 were the highest among all historical years simulated at all sites. During the recent warming (1999–2021), cumDDs >5°C from 1 November to the first predicted attack date in the spring averaged less than 800 for all sites, translating to very low probability for an extra overwinter generation (Figure 4b).

Simulations using modelled 30-year future climate normals suggest an increase in the number of summer generations relative to historical and contemporary periods that was associated with warming temperatures (Table 3). Mean annual temperature during the 2041–2070 normals period across sites was estimated to result in an increase of ∼0.7 WPB summer generations at the northern sites and ∼ 1.3 summer generations at the southern sites, relative to the historical (1900–1980) period. By 2071–2100, a projected mean annual temperature between 14.1°C and 17.3°C, depending on the site, was estimated to result in an increase of 1.2 to 1.5 additional summer WPB generations (Table 3). Similar to historical simulations, cumDDs >5°C from 1 November to the first predicted attack date the following spring suggests low probability for an extra overwinter generation in 2041–2070. By the end of the century at the warmest site, North Fork, a higher proportion of the population (70%) was predicted to complete an overwinter generation between 1 November and the predicted spring attack date.

DISCUSSION

Field observations of WPB adult attacks and brood emergence on individual trees at the Lassen site showed a single summer generation with a range of 0.05 to 0.39 emergence of a partial second generation in the fall of 2017 and 2018 (Figure 3). The majority of brood, however, overwintered and emerged the following spring resulting in two complete generations annually, one in the summer and one overwinter. A combined degree-day model developed with the observed data, predicting spring attacks and the number of summer generations, explained up to 74% of the variation in summer generations observed at the Lassen site, and up to 82% at the independent Stanislaus site. Model fit suggested an LTT of 5°C for development from egg to adult in the summer and 13°C for completion of development of the overwinter generation in the spring. The overwinter generation is likely made up of later instars (i.e., instar three, instar four, and prepupae), and the estimated LTT of 13°C is in the range of the relatively high-temperature threshold needed for WPB development from prepupa to pupae (∼12–15°C) (Miller & Keen, 1960). This threshold range for pupation, also found to be significant for a prepupal diapause in mountain pine beetle (Bentz & Hansen, 2018) and spruce beetle (Hansen et al., 2011), is a physiological adaptation that limits development during winter and reduces the chance for multiple annual generations in mountain pine beetle (Bentz et al., 2014; Bentz & Powell, 2014; Soderberg et al., 2021). Although prepupal diapause has not been investigated in WPB, the chance for multiple WPB generations overwinter is likely reduced, suggesting that potential increases in annual generations will be greater during summer in California temperate pine forests. At the Lassen field site, we did not observe evidence for more than a single successful WPB generation overwinter.

Model output using historical and contemporary temperature data highlights the annual variation in WPB voltinism that results from variation in annual temperatures. WPB voltinism was observed at multiple field sites in California during the dustbowl years in the late 1920s and 1930s, providing a direct comparison of our model results for the Modoc and North Fork sites, and a site just north of our Lassen site (Miller & Keen, 1960). During this time period, as expected, summer temperatures were above the historical 1900–1980 average (Figure 5). Our model output suggests a full summer generation at the Modoc and Lassen sites and close to two full summer generations at the warmer North Fork site, similar to that reported in Miller and Keen (1960). Observations in Miller and Keen (1960), however, also suggest there was some unquantified level of a partial generation during this time at each site, which matches with model results for the site near Lassen and the North Fork site, but less so for Modoc. Our field observations in 2017 and 2018 of attack timing and emergence are also within the range of historical reports, with a first summer emergence peak in June (resulting from the overwinter generation), peak emergence of a first summer generation in early August, and a partial second summer generation coinciding with a small emergence peak in September and October. In summary, our WPB model predictions are

generally consistent with WPB field observations during a historically warm and dry period in California (Miller & Keen, 1960).

Model simulations using historical and contemporary temperatures also highlight the dramatic trend in increasing summer temperatures beginning in the late 1990s at each of the sites, periods that were also linked with multi-year drought events in 2007–2009 and 2012–2015 (Pu et al., 2022) (Figure 5). Associated with these hotter drought events, an increase in the proportion of WPB brood with a partial second summer generation was predicted. By the year 2021, the predicted number of full and partial summer generations at all sites was the greatest since 1900, although the quantitative increase varied among the sites. The two most southern sites were the warmest on average and had the greatest increase from historical times (1900–1980). At the North Fork site one full summer and a 0.5 partial generation increased to two full and a 0.2 partial generation, and from one full and a 0.1 partial generation to two full and a 0.1 partial generation at the Stanislaus site (Table 2). In a modelling study that encompassed the North Fork and Stanislaus sites, Robbins et al. (2022) also predicted an increase in emergence of a partial generation during the 2012–2015 drought, relative to a historical period. A smaller change was predicted for the two northern and cooler sites where summer warming from historical to contemporary times was less. Lassen was predicted to increase from one full summer generation to one full and a 0.3 partial and Modoc to one full and a 0.4 partial (Table 2). Since 1980, climate analyses suggest that southern California has warmed faster than northern California, with the greatest temperature increase in summer and autumn (González-Pérez et al., 2022). Moreover, historical temperature records (Cluck, 2018) and model results (Robbins et al., 2022) suggest that WPB mortality during winter at CA sites has historically been infrequent. Undoubtedly, a combination of drought-stress to trees and an increase in the emergence of a partial summer generation associated with warmer summer and fall temperatures directly contributed to recent WPB-caused tree mortality in California (Koontz et al., 2021). Although we do not include the direct effects of drought-stress on trees, our model results highlight the important role of summer and fall warming on WPB voltinism.

Temperature projections using data from five GCMs and the high-emissions RCP 8.5 global warming scenario estimate potential future warming at the sites for two climate normal periods. As summer temperatures warm, the proportion of a population with a partial generation was predicted to increase in 2041–2070, and by the end of the century (2071–2100) projected temperatures at the Lassen and Modoc sites result in ~1.0 additional summer generation relative to the historical period, and ~ 1.6 additional summer and partial generations at the more southern North Fork and Stanislaus sites. Given that temperatures during winter are projected to not be warm enough for an additional generation, these results suggest that by the end of the century an estimated average annual temperature increase of ~6.3°C will result in a shift from 2.0 to 3.2 annual generations at the two northern sites and from 2.1 to 4.2 annual generations at the two southern sites, relative to the 1900–1980 historical period.

A WPB partial generation is a combined result of spring temperatures that influence the timing of first-generation tree attacks, and temperatures during summer and fall that dictate brood development and adult emergence timing of subsequent generations. Warm fall temperatures can result in emergence of some proportion of adults prior to winter, and the generation is considered partial because the remainder of brood overwinter in the tree and emerge the following spring or early summer. The contribution of a partial generation to population growth, however, will depend on success of the new tree attacks in the fall. At the Lassen site, we observed a small proportion of adults that emerged in the fall from trees attacked following the first summer generation. New attacks observed on trees at this time, however, were checked the following summer and found to be unsuccessful. In a modelling study, Robbins et al. (2022) estimated that contemporary temperatures increased the emergence of WPB partial generations by ~0.36 generations per year, which in turn increased ponderosa pine mortality by ~30%, relative to historical temperatures. Multiple historical observations also highlight that a partial generation can occur, although contribution to population success the following year has been difficult to quantify (Miller & Keen, 1960). The timing and number of adults in a partial generation that are available to attack new trees are likely threshold driven, given the need for mass attacks to overwhelm tree defences (Raffa et al., 2008). During times of drought when trees are stressed the contribution of these attacks to population success the following year is likely greater than during non-drought periods when new attacks on trees in the fall without sufficient numbers would be unsuccessful. Given that a partial generation is predicted to be common in future climates, additional research on this topic would add to our understanding of factors associated with the amount and timing of partial generations and if there is a threshold level of partial generation adults that contribute to WPB population growth and associated tree mortality. It is common for parent adults to re-emerge from brood trees to establish new egg galleries (Miller & Keen, 1960), and a greater understanding of the role these adults play in extended attack periods, in addition to the number and timing of a partial generation, is also needed. Additionally, data describing thermal developmental traits and a potential prepupal diapause would provide much-needed information on temperatures that limit an additional overwinter generation initiated from fall attacks.

CONCLUSIONS

WPB is a native bark beetle that can cause landscape-scale pine mortality within its western North America distribution. For example, during the recent 2012–2015 hot drought in California, 89.6% of ponderosa pine on study plots across four National Forests were dead and the primary culprit was WPB (Fettig et al., 2019). At four sites in California, our results highlight that the potential number of WPB generations annually is restricted by summer and fall temperatures, and that historical temperatures supported on average 1 to 1.5 full and partial summer generations. Field observations and degree-day model predictions show that recent warming associated with climate

change increased the number of generations, although to no greater than ~2 summer generations and one overwinter generation at the warmest of our study sites. By the end of the century, model projections indicate that >6°C warming will support one additional summer generation (totalling ~4 generations annually) at the warmest site and ~ 3 total generations annually at the cooler sites. A logical assumption has been that increasing temperature will result in an increase in the number of annual generations completed by multivoltine insects (Bale et al., 2002). Our results emphasize how the complexity between WPB thermal adaptations and response to changing climate may limit unconstrained increases in the number of annual generations, similar to that found for another *Dendroctonus* species (Bentz & Powell, 2014).

The role of a partial generation, wherein some proportion of adults emerge in the fall to attack new trees, in WPB population growth remains unclear although these generations are likely to be more successful during periods of drought stress on trees. WPB has an extensive distribution ranging from southern California, through parts of western Nevada, Washington, Oregon, Idaho, and western Montana, into southern British Columbia, Canada (Furniss & Carolin, 1977), and was recently separated from *D. barberi* which is found attacking ponderosa pine on the east side of the Great Basin southward into Mexico (Sullivan et al., 2021; Valerio-Mendoza et al., 2019). We acknowledge the application of our model is limited to the geographic area in central and northern CA where temperatures and WPB phenology data for model parameterization and evaluation were obtained. Given the geographic variability in physiological adaptations to local climates observed among other native bark beetle species with extensive distributions (Bentz, Hansen, et al., 2022; Soderberg et al., 2021), WPB likely has physiological adaptations to specific climates. Investigations into WPB thermal relationships across its extensive range are needed. Including the role of temperature-driven WPB population growth in ponderosa pine tree mortality will facilitate improved forest vegetation models aimed at predicting tree mortality in a changing climate.

AUTHOR CONTRIBUTIONS

Barbara Bentz: Conceptualization; formal analysis; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **Daniel R Cluck:** Conceptualization; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Beverly M Bulaon:** Conceptualization; methodology; writing – review and editing. **Sheri L Smith:** Conceptualization; methodology; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Daily maximum and minimum temperatures recorded at the Stanislaus site (a), number of western pine beetle (WPB) spring attacks and WPB emerged from trees during the summer generation

at the Stanislaus site in 2017 (b), WPB attacks following emergence of the 2017 summer generation; emergence from these trees was not monitored in 2018 (c), WPB summer attacks and emergence of the summer generation in 2018 (d), and WPB attacks following emergence of the 2018 summer generation and emergence from these trees in 2018; these trees were not monitored in 2019 (e). Shown are the mean and standard error among trees.

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