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Reviewed work(s):

Source: *The American Naturalist*, Vol. 179, No. 5 (May 2012), pp. E163-E171

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/10.1086/665007>

Accessed: 29/01/2013 14:49

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# Mountain Pine Beetle Develops an Unprecedented Summer Generation in Response to Climate Warming

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Submitted August 17, 2011; Accepted December 29, 2011; Electronically published March 22, 2012

**ABSTRACT:** The mountain pine beetle (MPB; *Dendroctonus ponderosae*) is native to western North America, attacks most trees of the genus *Pinus*, and periodically erupts in epidemics. The current epidemic of the MPB is an order of magnitude larger than any previously recorded, reaching trees at higher elevation and latitude than ever before. Here we show that after 2 decades of air-temperature increases in the Colorado Front Range, the MPB flight season begins more than 1 month earlier than and is approximately twice as long as the historically reported season. We also report, for the first time, that the life cycle in some broods has increased from one to two generations per year. Because MPBs do not diapause and their development is controlled by temperature, they are responding to climate change through faster development. The expansion of the MPB into previously inhospitable environments, combined with the measured ability to increase reproductive output in such locations, indicates that the MPB is tracking climate change, exacerbating the current epidemic.

**Keywords:** bark beetle epidemic, *Dendroctonus ponderosae*, global climate change, life-history change.

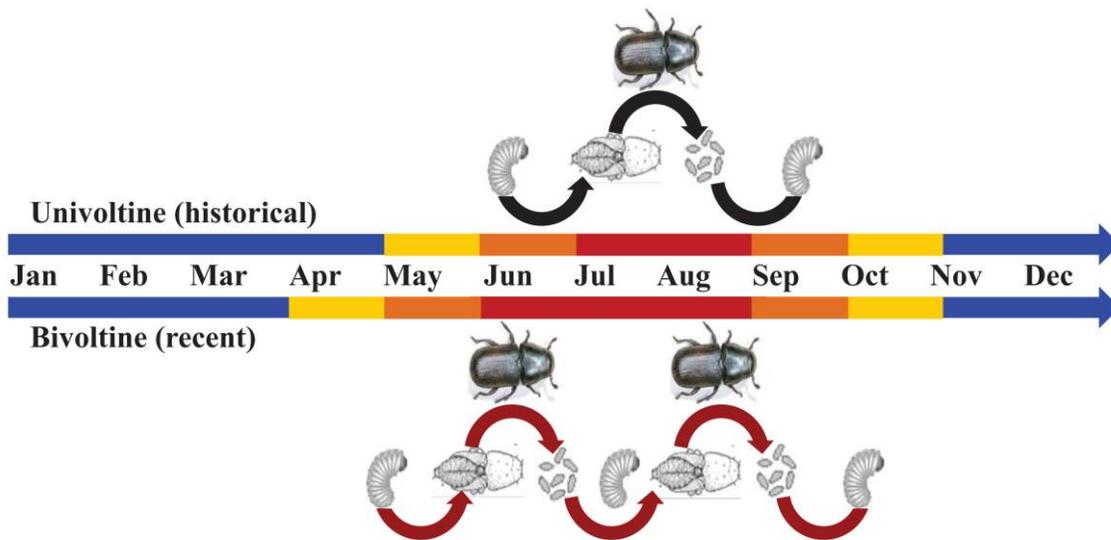
## Introduction

The mountain pine beetle (MPB; *Dendroctonus ponderosae*), is currently the most significant source of insect-caused mortality in mature forests in western North America, annually combining with other insects and pathogens to affect an area of forest orders of magnitude larger than that affected by fires (Wood 1982; Romme et al. 1986; Logan et al. 2003). An epidemic of the MPB has been spreading in pine forests of western North America for more than a decade, and in response to climate warming, the MPB is attacking trees at higher elevation and latitude than previously recorded (Aukema et al. 2008; Logan and Powell 2009; Robertson et al. 2009). The current MPB epidemic is the largest in history, extending from the Yukon Territory, Canada, to southern California and New

Mexico (Logan and Powell 2001; Taylor et al. 2006). The economic and ecological consequences of this epidemic are both profound and complicated (Raffa et al. 2008). To date, more than 13 million ha of trees have been killed in British Columbia (Kurz et al. 2008). The MPB-killed trees in British Columbia alone will release 990 million tons of CO<sub>2</sub> into the atmosphere, an amount equal to five times the annual emissions from all forms of transportation in the country (Kurz et al. 2008). Forests affected by bark beetles also have altered hydrology (Bewley et al. 2010; Pugh and Small 2011) and biogeochemical cycles (Huber 2005; Morehouse et al. 2008). Thus, extensive beetle kill is altering forest ecology and tipping conifer forests from regional carbon sinks to carbon sources, thereby creating positive feedback for climate-change factors.

Across the majority of its range, the MPB is historically univoltine (fig. 1), with the exception of semivoltine populations in the coldest environments of the MPB range at high elevation and latitude (Amman 1973; Wood 1982; Bentz and Schen-Langenheim 2007). Adult MPBs can successfully attack a wide range of true pines (Pinaceae: *Pinus*), including both native and introduced species occurring across approximately 25 latitudinal degrees and along altitudinal gradients of nearly 3,000 m (Bentz et al. 2010). In order to overcome pine resin defenses and to increase reproductive success, the MPB has evolved to emerge en masse, with females subsequently attacking host trees and releasing aggregation pheromones to coordinate mass attacks and attract mates (Borden 1982; Wood 1982; Raffa and Berryman 1983; Berryman et al. 1985, 1989). Females bore through the bark and into the cambial layer, severing resin canals and releasing a flow of resin that exudes from the borehole, forming an obvious “pitch tube” on the tree bark (Berryman 1972; Raffa and Berryman 1983; Raffa and Smalley 1995; Trapp and Croteau 2001). If the initial physical flow and chemical toxicity of resin are overcome, females excavate brood galleries in the phloem and inoculate the tree’s cambium with one or more species of blue-stain fungi (Six 2003; Six and Klepzig 2004; Six and Bentz 2007). Blue stains act as both a larval

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**Figure 1:** The historical mountain pine beetle (MPB) univoltine life cycle (above calendar arrows and linked by black arrows) and the observed MPB bivoltine life cycle (below calendar arrows and linked by red arrows). Calendar arrow colors represent monthly temperature regimes: blue for  $<0^{\circ}\text{C}$ , yellow for  $0^{\circ}\text{--}4.99^{\circ}\text{C}$ , orange for  $5^{\circ}\text{--}9.99^{\circ}\text{C}$ , and red for  $10^{\circ}\text{C}$  and higher.

food source (Six and Paine 1998; Bentz and Six 2006) and can also help to locally exhaust tree defenses, aiding the MPBs in killing the host tree (Raffa and Berryman 1983; Berryman et al. 1989). Although the fate of the tree is decided shortly after a mass attack, infested trees retain their needles (Morehouse et al. 2008) and appear green until the following growing season. Thus, MPBs historically developed and overwintered as larvae in trees that appear, from a distance, to be healthy and emerged as adults from fading trees the following summer (Mitton and Sturgeon 1982).

Records of MPB flights in lodgepole pine (*Pinus contorta*) forests of Utah, and in British Columbia indicate some historical variations in flight inception, with the earliest reported emergences occurring on June 16 (Reid 1962). Records also indicate that peak flights typically occurred in the latter weeks of July and early August and that no flights occurred after August 20 for any surveyed locations (Reid 1962; Safranyik and Jahern 1970; Rasmussen 1980). Historical documentation of MPB flight patterns in Colorado are rare, but U.S. Forest Service reports indicate that the MPB flight season in ponderosa pine forests of Colorado lasted for approximately 7 weeks, with peak flights during the second and third weeks of August (McCambridge 1964). Historical records of MPB flight timing and duration for Colorado lodgepole pine forests are unavailable (Tishmack et al. 2005), but a recent study in a forest at similar elevation 30 km southwest of our study site reported similar results, with infrequent

emergences in July, large numbers of MPBs flying between August 5 and 19 and a flight season of approximately 50 days (Tishmack et al. 2005).

Despite such recent reports, on June 2, 2008, we observed MPBs flying and attacking pines at an elevation of 3,020 m at the University of Colorado's Mountain Research Station (CU-MRS) on Niwot Ridge, Boulder County, Colorado. These observations suggested that the MPB life cycle had changed substantially, with the flight season beginning more than a month earlier than the historic norm. The early flight inspired us to test three null hypotheses: (1) temperatures had not changed in the last 4 decades at that site, (2) the length and timing of the flight season of the MPB had not changed, and (3) the life cycle had not changed, and the MPB was still univoltine.

### Material and Methods

To test our first hypothesis, that temperatures had not changed at our study site, we used long-term hourly temperature data collected from the CU-MRS C-1 climate station (9.7 km east of the Continental Divide,  $40^{\circ}02'09''\text{N}$ ,  $105^{\circ}32'09''\text{W}$ ), at 3,021 m on Niwot Ridge. Because of the availability of a previous report published in the 1970s that detailed the MPB elevational range in the U.S. Rocky Mountains, we used temperature data from 1970 to 2008 (our first year of observation). Annual mean air temperatures, annually accumulated temperatures (sum of daily

means), and total days with a temperature greater than 0°C were calculated from daily mean air temperatures for each year. Degree-days for MPB development were calculated by subtracting the previously reported threshold of 5.5°C from daily mean temperatures and then transforming negative values to 0 before summation (Hicke et al. 2006). Statistical analyses were completed on data binned into decades and compared via fixed-effects ANOVA. Decades were considered as fixed effects, and multiple means comparisons were completed with Tukey's HSD tests.

To test our second hypothesis, in 2009 we established a 40 × 50-m study site approximately 100 m from the UC-MRS C-1 climate station along a mixed-conifer ridge-top. The site has a variable southern aspect and is dominated by the common MPB host trees lodgepole pine *Pinus contorta latifolia* and limber pine *Pinus flexilis*. During the summers of 2009 and 2010, we measured MPB flight season inception and duration with three 12-funnel Lindgren flight traps baited with MPB aggregation pheromone purchased from Contech Enterprises (Victoria, British Columbia, Canada). The longer axis of the study site has an east-west orientation, and we placed the traps in a triangular pattern near the southeastern, southwestern, and northwestern corners of the study site. We hung the traps in understory gaps by suspending them from canopy tree limbs, with the bottom funnel and collection cup ranging from 1.0 to 1.5 m above the ground surface.

To test our third hypothesis, that MPB generation times had not changed, we used MPB aggregation pheromones to induce brood establishment in trees with no evidence of prior MPB attacks and then monitored MPB brood development by removing bark to observe MPB development at intervals throughout the summer and fall of 2009 and 2010. We included both limber and lodgepole pines in our study because the MPB was attacking both pine species near our study site. To certify pines as having no prior MPB attacks, we completed an early spring census in 2009 and located 50 trees (50 : 50 ratio of lodgepole and limber pines) with no evidence of prior MPB attacks such as pitch tubes or entrance/emergence holes in the bark. We chose trees with moderate to large diameters (>25 cm diameter at breast height) and a spatial arrangement that covered the largest possible extent of the site and then marked each tree with a unique identification number on an aluminum tag. After tree certification, we placed MPB aggregation pheromone packets both in the Lindgren funnel traps, as described above, and directly onto the boles of seven certified trees that were chosen because they were located near trees with existing MPB broods under the bark.

We began censuses of the site on June 8, 2009, and May 23, 2010, and continued censuses into late September 2009

and mid-October 2010. We visited the site once every 7–14 days in 2009 and at more frequent intervals of 48 or 72 hours in 2010. During each census, we removed all insects from the trap cups, which contained 70% ethanol to prevent MPBs from escaping and to keep predators from devouring the trapped insects, and we also examined all certified trees. Early censuses recorded the date of first MPB attacks, while later in the season we were dissecting small portions of galleries in the lower 2 m of tree boles to determine which life stages were present and to note evidence of emergence. We did not attempt to estimate what proportions of life stages were present or to quantify detailed differences in MPB development between limber and lodgepole pines, for that would have required extensive destructive sampling. Our goal was to watch the progression of the life stages during the summer to determine with certainty that eggs deposited in June could complete development in the same season. All seven trees were attacked in June each year, and detailed monitoring of MPB brood development focused on five trees in 2009 (four limber pines and one lodgepole pine) and seven trees in 2010 (all limber pines). Two trees were excluded in 2009, one limber pine and one lodgepole pine, because they did not have evidence of successful MPB development and emergence. We did not dissect certified trees in June 2009 or 2010 for fear of destroying nascent galleries, but we did examine trees at the margins of our site that had been attacked the previous summer, to determine which life stages were present in early and mid-June.

## Results

The long-term temperature records taken approximately 100 m to the west of our study site showed significant warming from 1970 to 2008; the trend was not linear over time, but temperatures and/or heat energy available for MPB development increased substantially (table 1) and led us to reject our first hypothesis. The mean annual temperature in the past 2 decades was 1.5°C warmer ( $P < .0001$ ) than that in the previous 2 decades (table 1). Similarly, the mean cumulative temperature before July 1 increased 296.2°C per year ( $P < .001$ ) in the past 2 decades from that in the previous 2 decades (table 1). Air temperatures during MPB spring development warmed significantly, with the annual number of days above 0°C before July 1 increasing by 15.1 days ( $P < .01$ ) in the past 2 decades. Annual MPB-growing degree-days showed a similar trend and increased by 249.5 days, or 43.7% ( $P < .0001$ ), from the decade beginning 1970 to the most recent decade; degree-days before July 1 increased by 57.9% over the same period. Thus, average temperature has increased at the MPB site, and the trend is clearly evident before

**Table 1:** Bark beetle study site air temperature metrics by decade

| Variable                               | 1970–1979                  | 1980–1989                  | 1990–1999                  | 2000–2008                 | <i>P</i> |
|--|----------------------------|----------------------------|----------------------------|---------------------------|----------|
| Annual temperature (°C)                | 1.07 (.1) <sup>A</sup>     | 1.05 (.1) <sup>A</sup>     | 2.32 (.1) <sup>B</sup>     | 2.70 (.2) <sup>B</sup>    | <.0001   |
| Days with mean temperature >0°C        | 78.3 (3.6) <sup>A</sup>    | 80.0 (5.0) <sup>AB</sup>   | 93.1 (3.9) <sup>AB</sup>   | 95.4 (3.1) <sup>B</sup>   | <.01     |
| Accumulated temperature (°C) to July 1 | −260.1 (51.0) <sup>A</sup> | −252.7 (79.7) <sup>A</sup> | 17.7 (50.1) <sup>B</sup>   | 61.7 (53.8) <sup>B</sup>  | <.001    |
| Total annual DDs                       | 570.6 (26.2) <sup>A</sup>  | 584.8 (53.0) <sup>AB</sup> | 722.6 (25.5) <sup>BC</sup> | 820.1 (36.4) <sup>C</sup> | <.0001   |
| DDs before July 1                      | 128.4 (10.7) <sup>A</sup>  | 135.0 (22.9) <sup>A</sup>  | 175.5 (16.8) <sup>AB</sup> | 202.7 (16.5) <sup>B</sup> | <.02     |

Note: Values are annual means ( $\pm 1$  SE) for the decade. Values with different superscript letters are significantly different, according to Tukey's HSD ( $P < .05$ ). Probability values from ANOVA are shown in the last column. DD = degree-days for development, calculated from a threshold of 5.5°C.

July 1, which is particularly relevant to the early flight of MPBs.

The Lindgren funnel trap captures revealed significant changes in the MPB flight season, leading us to also reject our second hypothesis. We recorded the first MPBs in traps on June 17, 2009, and June 21, 2010 (table 2; a conservative estimate of first emergences), and we observed MPBs in the act of emerging from trees on May 26, 2010 (a liberal estimate of first emergence). The last MPBs were removed from traps on September 20, 2009, and October 4, 2010. These observations revealed that the MPB flight seasons in 2009 and 2010 began approximately 6 weeks earlier and lasted twice as long as those previously reported (fig. 1; table 2).

We rejected our third hypothesis—which was tested by monitoring brood development in the trees that were first attacked in June of both 2009 and 2010—because of the observation of an unprecedented summer generation of MPBs in some broods observed in both limber and lodgepole pines. Specifically, in four trees in 2009, the larval galleries were variably developed, containing empty pupal chambers connected to exit boreholes along with larvae, pupae, and adults. In the fifth tree, there were no remaining larvae, and all successful development chambers had exit holes bored through the bark. This pattern was repeated in 2010, with all seven trees receiving initial attacks in June and releasing some adults by the time of survey in September. Importantly, all trees had been attacked for the first time in June and had released adult MPBs by August or September, and their needles were still green during our final survey in November. In addition, in early and mid-June 2009 and late May 2010, when we removed bark from trees that had been attacked the previous summer, we found late-instar larvae, pupae, teneral or incompletely pigmented adults, and fully pigmented adults digging exit tunnels (dated photographs are available from J.B.M.). This observation indicated that the flight-trap captures noted above were likely to contain samples that included recently eclosed adults.

All baited trees and many other trees were attacked during the months of June, July, and August, and most trees that were attacked in June accrued additional attacks

later in the summer. All of the attacked trees had green needles in the fall, further insuring that all galleries in certified and baited trees were established in the same calendar year, for if they had been attacked in the previous summer their needles would have turned yellow in early summer.

## Discussion

After decades of increasing temperatures, particularly in the spring, the upper elevational limit of MPB attacks in Colorado has increased from roughly 2,740 m to more than 3,350 m. Our detailed observations over two consecutive years revealed that the flight season has roughly doubled in length and that a portion of the population is now bivoltine. Egg galleries are being initiated more than a month earlier than they were several decades ago, thus enabling MPB eggs laid in June or July to develop into adults during the warmest months of the year.

While our study was limited in area, it was completed in a site that was characterized as climatically unsuitable for MPB development by the U.S. Forest Service only 3 decades ago (Amman 1977; Amman and Schmitz 1988). Also, an anecdotal observation indicated that the summer generation was also occurring in ponderosa pine *Pinus ponderosa*. In a nearby field site roughly 200 m lower in elevation, we documented a ponderosa pine attacked between July 19 and 25, 2010. We examined MPB devel-

**Table 2:** Sampling effort and mountain pine beetle (MPB) flight and emergence time lines for 2009 and 2010

| Event                          | 2009         | 2010       |
|--------------------------------|--------------|------------|
| Start of trapping and census   | June 8       | May 21     |
| First trap capture             | June 17      | June 21    |
| Last trap capture              | September 20 | October 4  |
| First MPB attacks              | June 8       | June 27    |
| Last site census               | November 14  | October 31 |
| Trees with summer generation   | 5/7          | 7/7        |
| Length of flight season (days) | 95           | 105        |

Note: "Trees with summer generation" means the ratio of trees with the emergence of a second generation to trees baited.

opment from approximately five broods on September 22, 2010, and found that 13%–17% of the MPBs in these galleries were adults, and there was evidence of previous mass emergence on all quadrants of the bottom 2 m of the trunk. Emerging adults had developed from eggs laid in July of the same summer. Thus, we observed the summer generation in lodgepole, limber, and ponderosa pines.

Early flight of MPBs has been recently reported from Idaho (Bentz 2006; Bentz and Schen-Langenheim 2007) and Wyoming (Logan et al. 2010), but ours is the first report of a summer generation in the MPB. The potential for increasing temperature to extend the range of the MPB and increase its development rate, especially at higher elevations, was previously recognized and presaged by models of adaptive seasonality (synchronous emergence of adults; Logan and Powell 2001; Carroll et al. 2004; Hicke et al. 2006; Bentz et al. 2010). These models predict that warming will reduce adaptive seasonality in most areas, leading to maladapted lengthening of the MPB flight season and thereby decreasing MPB establishment. The extensive MPB kill now found across widely variable forests and in novel ranges at higher elevations and latitudes than ever before suggests not only that MPB establishment and reproduction under warming conditions remain highly successful but also that warming has not caused widespread maladaptive change in the MPB life cycle.

Evidence for climate-driven changes in life history and range has also been noted in other areas and in other *Dendroctonus* bark beetles. MPBs in the Greater Yellowstone ecosystem are shifting from a semivoltine (one generation per 2 years) life cycle to a univoltine life cycle (Logan et al. 2010). Populations of the spruce beetle *D. rufipennis* have decreased their development time, switching from semivoltine to univoltine (Berg et al. 2006). Recent outbreaks of southern pine beetle *D. frontalis* in forests far north of its historic range in the eastern United States seem to be explained by an increase of 3.4°C in minimum winter air temperatures in the eastern United States from 1960 to 2004 (Tran et al. 2007). Models of population dynamics predict that *D. frontalis* will increase its number of generations per year as the climate warms (Waring et al. 2009).

Logan et al. (2010), characterizing the effect of climate change on MPB in the Greater Yellowstone ecosystem, stated, “The result is a bi-peak emergence of early, re-emerged beetles and a later traditionally timed brood. The combination of a warming climate and apparent vulnerability to attacking beetles has resulted in a shift from nonoverlapping, semivoltine (life cycle requiring two years to complete) generations to overlapping, bimodal, univoltine generations with a concomitant increase in reproductive potential” (p. 899). Computer simulations modeling these changes revealed that “broods produced by

re-emerged adults may experience enough thermal energy to complete the life cycle within the same year of attack” (J. A. Logan, unpublished data). Our field studies in 2009 and 2010 are consistent with these computer simulations, but our interpretation of the change in the life cycle differs from that of Logan et al. (2010) in an important way. Biologists who have seen the early flights of MPBs (Bentz 2006; Bentz and Schen-Langenheim 2007; Logan et al. 2010) have assumed them to be MPBs that had initiated galleries the previous summer, overwintered as adults, and reemerged to attack another tree to produce a second gallery. While we do not reject that some adults might survive the winter to emerge the following spring, our dissections of trees in May and June revealed pupae and teneral adults, clearly indicating that the broods from the previous summer were developing faster and emerging earlier, in May and June rather than in July and August. Furthermore, these young adults lay eggs within a few days, and at least some of those eggs develop quickly over the summer to produce adults emerging in August and September. A consequence of the distinction between interpretations is that potential fecundity for reemerging adult MPBs is doubled, but if broods are bivoltine, then MPB fecundity has increased exponentially.

Rapid change in MPB life history in response to climate warming is possible because MPBs do not diapause and because their developmental rates are influenced by both temperature and genetics. When placed in a controlled environment, MPBs from northern populations developed to adults 3–6 weeks sooner than MPBs from southern populations (Bentz et al. 2001), and temperature-dependent differences in developmental rates were attributable to additive, dominance, and epistatic components of genetic variation (Bentz et al. 2011).

Further inference of genetic variation for developmental rate can be taken from a compilation of studies on degree-days required for MPB development from egg to adult, which varied from 278 to 812 degree-days (Carroll et al. 2006). Safranyik et al. (1975) reported the threshold temperature for development to be 5.5°C, and this threshold was used here to calculate degree-days and by Carroll et al. (2004) in their model of MPB development. However, the experimental evidence of heritable genetic variation for developmental rate (Bentz et al. 2001, 2011; Carroll et al. 2006) suggests that either the threshold temperature for development or growth rates, or both, would be variables subject to selection to adapt populations to their local environments. Selection for temperature-dependent development has been experimentally documented in other holometabolous insects living along temperature clines, for example, *Rhagoletis* flies (Michel et al. 2010), and recent studies of copepods indicate that development has stronger temperature dependence than does growth

rate across all life stages of these ectotherms (Forster et al. 2011). Assuming similarities between other ectotherms and bark beetles, models of MPB responses to climate change would have to incorporate this variability to accurately predict population dynamics.

If warming temperatures caused multivoltinism to develop at high elevation, why are populations in warmer regions, lower elevation, and lower latitudes not commonly multivoltine? The answer likely involves elevational and latitudinal clines in both the selection pressure for MPB synchronous emergence and the selection on pine tree defenses and physiology.

The ability of pine trees to produce and store resin, the primary defense against the MPB, is a function of water availability (Cates and Alexander 1982; Wallin et al. 2003); droughts and seasonal dry periods reduce resin pressures, increasing the probability of successful bark beetle attacks. Historic MPB peak flights occurred in August, a dry portion of the growing season. While snow melts earlier at low elevation, presumably extending the time of susceptibility to MPB, pines from low elevation tend to withstand drought stress better than their high-elevation congeners (Zhang et al. 1997). Selection for MPB synchronous emergence to overcome pine resin defense while trees are in their most vulnerable physiological state has likely created the similarity in emergence patterns across elevation, but these patterns are probably underlain by gradients of MPB growth rates in contrasting thermal environments, similar to the genetic differences with latitude (Bentz et al. 2001). To synchronize emergence in the second and third week in August, populations in high, cool environments would need to reach maturity faster at specific temperatures or have lower threshold temperatures for development. Thus, MPBs at high elevations would need fewer degree-days to reach maturity and would have a greater response to equivalent increases in temperature.

Historical patterns of MPB attacks may have produced elevational patterns of host tree resistance to MPB attacks. Pines that dominate at low elevations, such as ponderosa pine, also occur within the historical range of the MPB and have likely been selected for greater resin defenses. Evidence of MPB selection on pine defenses comes from studies showing that pines possessing more-toxic resin and those that allocate more energy to resin-duct production have a greater probability of surviving bark beetle infestation (Sturgeon and Mitton 1986; Kane and Kolb 2010). The selection for resistance to MPB attack would make lower-elevation pines more difficult to colonize than higher-elevation pines. With a 2,740-m historical upper range limit (Amman 1973, 1977; Amman and Schmitz 1988), MPBs in our study site, for example, are attacking trees with little or no history of selection for defense. A 2011 pilot study supports our prediction of fewer tree

defenses with increasing elevation; both limber and ponderosa pines from below 2,070 m had more resin ducts per annual growth ring than pines from above 2,070 m (S. M. Ferrenberg, unpublished data). Thus, we hypothesize that pines above 2,740 m are less resistant to the MPB than those at lower elevation. Second, we hypothesize that fewer MPBs will be needed to cause tree mortality above 2,740 m, because of the lower resistance of the trees, placing less selective pressure on synchronized attacks and positively selecting for faster development/growth.

The combined effect of selection for rapid development in high-elevation MPB populations and the limited history of selection for host tree resistance would promote MPB range expansion into unexploited high-elevation forests, a trend reported in the literature. High-elevation MPB populations are adapted to colder climates than low-elevation MPBs, and these phenotypic traits would interact with climate warming to promote an extended flight season and enable the shift from one to two generations per year reported here. The proportional effect of warming temperatures would vary among populations, differing in genetically determined development rates related to climatic gradients. For these reasons, we predict that high-latitude and high-elevation populations should demonstrate the greatest response to an increase in development degree-days, while low-elevation populations would have a lesser response.

## Conclusions

Recent empirical observations and established conceptual models inspire a new perspective on the dynamic adaptation of the MPB to its environment. Expansion of the MPB's range higher in latitude and elevation than ever before and the development of a summer generation are responses of a genetically variable species, already adapted to heterogeneous environments, to climate change. Evidence of climate change is indisputable (Parmesan 2006, 2007; table 1), and genetic variation within and among populations of the MPB can be inferred from the great range of degree-days needed to complete development among populations (Bentz et al. 2001), variation in development that we observed among individuals within broods of the summer generation, and the general synchrony of emergence among populations along an elevational transect. Synchrony of MPB emergence along an elevational gradient suggests countergradient variation (Levins 1968; Connover and Schulz 1995) or genetic variation opposing the environmental effects of temperature on development, for if MPBs from colder environments emerge simultaneously with those from warmer environments, then MPBs in colder environments complete development with fewer degree-days. Roff (1980) modeled

life histories of insects adapting to a cline in growing season length and found that extending larval development to produce larger adults could accommodate smaller increases in the growing season. As the growing season became still longer, however, the insects responded by producing more generations per growing season. Those projections can be applied to increases in the growing season over years at a site to anticipate the appearance of a bivoltine life cycle in the MPB. The majority of insect responses to climate change involve altered responses to seasonal cues rather than adaptation to higher temperatures (Bradshaw and Holzapfel 2008). With its lack of diapause, the MPB may be altering responses to seasonal cues. Alternatively, selection for faster development and the consequent increase in fitness might be interacting with rapid climate change to increase rates of MPB development, particularly in life zones where MPBs are adapted to historically low temperatures.

#### Acknowledgments

D. Bright identified bark beetles. M. Barlerin, S. Barlerin, and A. Faist assisted with MPB trapping and tree surveys. Logistical support and temperature data were provided by the National Science Foundation-supported Niwot Ridge Long-Term Ecological Research project and the University of Colorado Mountain Research Station. Funding was provided by Department of Energy grant DE-FG02-07ER64457, Boulder County Parks and Open Space, the John Marr Fund, and the Indian Peaks Wilderness Alliance. D. Leatherman provided comments throughout the study, and J. Harte, A. Hirsh, L. Kueppers, J. Langenhan, D. Leatherman, Y. Linhart, A. Martin, R. Monson, and P. Nosil contributed comments on drafts of the manuscript. The manuscript was substantially improved by suggestions from two anonymous reviewers.

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Natural History Editor: Craig W. Benkman



Left, mountain pine beetle *Dendroctonus ponderosae*; right, Berthoud Pass, at an elevation of more than 11,000 feet, showing a swath of dead trees that goes essentially all the way to Wyoming, a distance of approximately 50 miles. Photographs by Jeff Mitton.