Comment

Mountain Pine Beetle Seasonal Timing and Constraints to Bivoltinism

(A Comment on Mitton and Ferrenberg, "Mountain Pine Beetle Develops an Unprecedented Summer Generation in Response to Climate Warming")

Barbara J. Bentz[1,*] and James A. Powell[2]

1. USDA Forest Service, Rocky Mountain Research Station, Logan, Utah 84321; 2. Utah State University, Department of Mathematics and Statistics, Logan, Utah 84321

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abstract: Mountain pine beetle tree colonization typically occurs in July and August, with completion of a generation one (univoltinism) or two (semivoltinism) years later. In a 2012 publication, Mitton and Ferrenberg suggested that climate change resulted in an unprecedented generation between June and September (a summer generation), with a concomitant shift to two generations in one year (bivoltinism). Although summer generations are not uncommon in this species, completion of a second generation across winter, between September and June, would be required for bivoltinism, a phenomenon not previously observed. Mitton and Ferrenberg showed that a summer generation can occur, but they failed to adequately track cohorts and provided no compelling evidence for bivoltinism. We demonstrate that a winter generation—and hence bivoltinism—would have been physiologically impossible at the high-elevation site used in Mitton and Ferrenberg due to lower thermal developmental thresholds. The mountain pine beetle is indeed being influenced by climate change. To address the challenges of future population outbreaks of this significant tree mortality agent, however, it is imperative to consider evolved, thermally dependent traits that serve to maintain seasonality.

Keywords: climate change, *Dendroctonus ponderosae*, seasonality, voltinism.

Introduction

Recent changes in climate and the associated ecological effects are undeniable (Intergovernmental Panel on Climate Change 2013). Climate change is contributing to measurable alterations in species distributions and phenology (Parmesan 2006; Thomas 2010). Short generation times and a strong connection between developmental processes and temperature make insects particularly sensitive to warming associated with climate change (Bale et al. 2002). Many insect species, including native insects deemed pests due to their economic impact, have responded positively to recent warming. A prime example is the mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins; Coleoptera: Curculionidae, Scolytinae), a native bark beetle that has caused more tree mortality in western North American conifer forests than any other agent over the past few decades (Meddens et al. 2012). At the northern and southern edges of its geographic distribution, the MPB is limited by climate rather than host trees, and outbreak-level activity has recently occurred farther north than previously reported, likely as a result of climate warming (Safranyik et al. 2010). Sustained population outbreaks are now also occurring in high-elevation forests, where persistent activity was previously constrained by cold temperatures (Amman 1973; Logan and Powell 2001). Warming winters increase brood survival (Régnière and Bentz 2007), and at high elevations warming summers allow some individuals to shift from one generation every two years to one generation every year (Bentz et al. 2014). Thus, it is clear that climate warming is influencing this insect.

In their article "Mountain Pine Beetle Develops an Unprecedented Summer Generation in Response to Climate Warming," Mitton and Ferrenberg (2012) claim that recent warming has allowed the MPB to complete an unprecedented generation in a single summer (i.e., between June and September) and that a shift to bivoltinism (i.e., two generations in one year) was a direct result. Although summer generations are not uncommon for this species (DeLeon et al. 1934; Reid 1962), a second generation that

* Corresponding author; e-mail: bbentz@fs.fed.us.

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occurs across winter (i.e., between September and June) would be required for bivoltinism. Mitton and Ferrenberg (2012) did not adequately track the timing and occurrence of MPB cohorts within trees and thereby provide no compelling evidence that a winter generation—and hence bivoltinism—occurred. Bivoltinism is a life-history strategy not previously documented in the field for this species, and semivoltinism (i.e., one generation every two years) was most likely the historically predominant life cycle at their 3,020-m study site in central Colorado. A climate-driven shift of this magnitude could be the harbinger of a catastrophic regime change for the MPB. As such, it is important to understand whether and where this type of shift might occur and to carefully consider purported observations of such shifts.

We review the evidence provided by Mitton and Ferrenberg (2012) supporting their claim that the MPB is exhibiting bivoltinism and propose alternative—and more likely—explanations for their observations. In addition to highlighting evolved developmental traits that could constrain completion of a generation across winter, we use daily temperature data from the study site used by Mitton and Ferrenberg (2012) to drive a model that describes MPB phenology and voltinism (Powell and Bentz 2014). Model predictions and knowledge of thermally driven life-history traits confirm the improbability of MPB bivoltinism during the years of their study. Temperatures have warmed over the last 35 years at the study site of Mitton and Ferrenberg (2012), although according to results from our model simulation not enough to result in a bivoltine life cycle. When evaluating the potential for climate change–induced alterations in MPB life-cycle timing, it is important to adequately track the timing and occurrence of cohorts and to consider life-history traits that have evolved to promote population success in varying environments.

MPB Ecology

MPB is a native species that infests trees within *Pinus* and has an expansive distribution from Baja California Norte, Mexico, to northern British Columbia and western Alberta, Canada, and east into South Dakota and western Nebraska (Wood 1982; Costello and Schaupp 2011). Range expansion northward is ongoing as a result of both winter and summer warming (Cudmore et al. 2010; Sambaraju et al. 2012). Similar to other *Dendroctonus* species, the MPB is capable of irruptive population dynamics caused by both density-dependent and independent processes (Berryman 1982; Boone et al. 2011; Martinson et al. 2013), and the host tree is almost always killed in the process of colonization and brood development within the phloem. MPBs feed within the phloem, moulting through four larval instars before making a pupal chamber where pupation occurs. Prior to emerging from a tree to disperse and attack new live trees, teneral adults mature by feeding on nutrient-rich spores of fungal symbionts within the pupal chamber (Bleiker and Six 2007). After "brood adults" emerge and disperse to attack a new tree, mating occurs and eggs are oviposited. At this point, we refer to these adults as "parent adults." Parent adults can reemerge, disperse to attack another tree, and oviposit an additional cohort of eggs. This reemergence can occur immediately following a first attack, or parent adults can overwinter and reemerge in early summer (Reid 1962).

Plasticity in MPB developmental timing results in univoltinism (i.e., one generation every year) at low elevations and a mix of univoltinism and semivoltinism (i.e., one generation every two years) at high elevations (Hopkins 1909; Reid 1962; Amman 1973; Bentz et al. 2014). Their phenology is temperature dependent (Bentz et al. 1991; Régnière et al. 2012) and the timing of brood adult emergence and flight varies among years and sites, but historically it has been reported to occur from July through August (Safranyik and Carroll 2006). This attack timing allows oviposition and larval growth to occur so that the life stages most vulnerable to cold (i.e., eggs and pupae) are not present in winter in the coldest habitats (Reid and Gates 1970; Logan and Bentz 1999). Synchronization of adult emergence is key to the mass attacks required to overwhelm the defenses of live trees (Logan and Bentz 1999; Boone et al. 2011) and is facilitated through larval thresholds for development that differ among the instars (Jenkins et al. 2001). Genetic differences in development traits across a latitudinal cline suggest that adaptation to local climates has occurred (Bentz et al. 2001, 2011; Bracewell et al. 2013). Selection on temperature-dependent traits that promote univoltinism is apparent across a large range of thermal environments, including warm habitats at low latitudes (Bentz et al. 2014).

MPB Voltinism

Voltinism describes the number of generations an organism completes in a single year (Danks 2007). Species in warm habitats often have the capacity to produce two or more generations in a year (i.e., bivoltinism and multivoltinism), whereas species in cooler habitats often require one (i.e., univoltinism) or two (i.e., semivoltinism) years to complete a single generation. For herbivorous forest pest species, shorter generation time can lead to increased population growth that results in increased tree mortality and therefore has important economic and ecological implications. Measuring voltinism in insects is complex, however, particularly when based on field observations. Brood initiated at the same time can have varying life-cycle du-

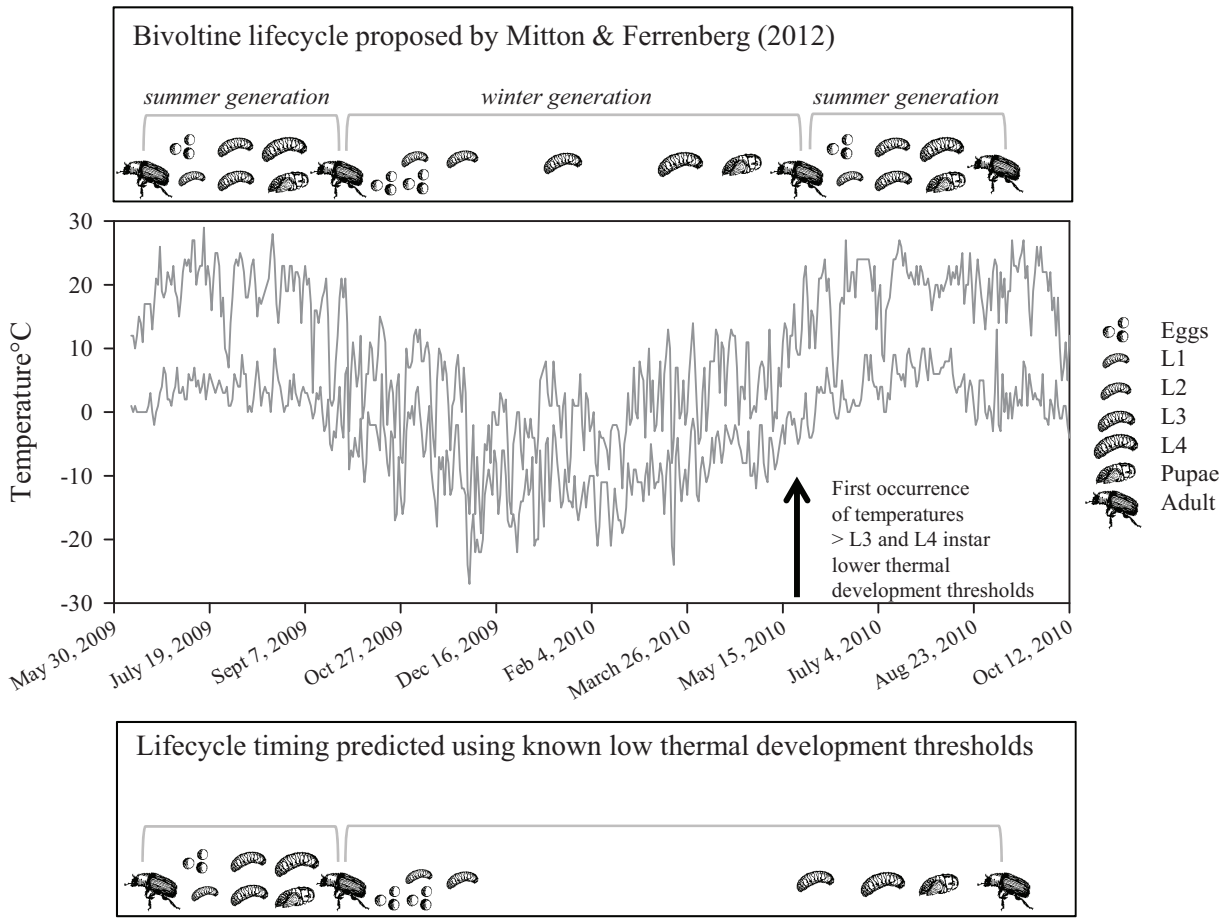

Figure 1: Mitton and Ferrenberg (2012) proposed that mountain pine beetles (MPBs) completed a bivoltine life cycle (i.e., two generations in one year) between June 2009 and June 2010 (*top panel*). Although a summer generation can occur in warm years when overwintered adults emerge in June, a second generation across winter from September 2009 to June 2010 at the Niwot Ridge site would have been physiologically impossible due to temperature-dependent thermal thresholds. Temperatures at the site remained below thresholds that permit larval development across winter, and temperatures above third-larval (L3) and fourth-larval (L4) instar low-development thresholds (see fig. 2) did not occur until late May 2010 (*middle panel*), restricting completion of a generation prior to early June 2010. Instead, we predict that a second generation would require the warm temperatures in summer 2010 to complete development, with the earliest adult emergence in August and September (*bottom panel*)—a univoltine life cycle, not bivoltine.

ration when factors such as temperature partitions the brood into distinct groups known as cohorts. For example, a brood can be split into univoltine and semivoltine cohorts when genetic variation in thermal requirements and microclimatic variation in temperature allow some individuals to complete a life cycle faster than other individuals from the same brood. MPBs, with oviposition often extended across several weeks, are particularly prone to cohort splitting. To characterize voltinism, it is critical to distinguish among cohorts (Danks 2007). For the MPB, that means knowing when a tree was attacked and broods were initiated.

Hopkins (1909) was the first to report on overlapping cohorts in the MPB. DeLeon et al. (1934) further observed that a mix of univoltine and semivoltine cohorts, in addition to reemerged parents, could be found dispersing and attacking trees throughout the summer, often at the same time. The MPB does not have an obligatory diapause, and multiple life stages can overwinter. Although the main flight period for univoltine MPB brood adults has been historically described to occur in July and August, a result of overwintering in the larval stage, it is not uncommon to also find parent adults and semivoltine brood adults dispersing earlier. For example, parent adults that overwinter can reemerge in early June to disperse and make a second attack on new trees. These trees could also be under attack by new brood adults from a semivoltine cohort that also overwintered and emerged in early June. In

both cases, the adults that emerged in June overwintered as an adult and were able to emerge early because development was completed prior to winter. In warm years, trees attacked in June can produce broods that complete development and potentially emerge the fall of the same year (Reid 1962; Bentz et al. 2014), referred to as a summer generation by Mitton and Ferrenberg (2012). Adults that emerge and disperse in June, however, are usually relatively few in number (Bentz 2006).

Pheromone traps have been used to monitor bark beetle dispersal timing and voltinism, but it is difficult—if not impossible—to assign a cohort identity to a captured adult. Moreover, pheromone traps are likely to disproportionately sample the dispersing population when few adults are flying. When few adults are dispersing to attack new trees, as often occurs in June, natural pheromone production from infested trees is low. Pheromone traps therefore have little competition and are correspondingly more attractive for the few dispersing beetles. This inflates the estimated number of adults relative to the trap catch during the main dispersal period (Bentz 2006).

MPB Voltinism Proposed by Mitton and Ferrenberg (2012)

A goal of Mitton and Ferrenberg (2012) was to describe MPB voltinism at a high-elevation pine site at 3,020 m on Niwot Ridge in central Colorado. On the basis of adult catch data from three pheromone traps and periodic life-stage sampling of seven trees baited with aggregation pheromones in June, Mitton and Ferrenberg (2012) asserted that the timing of MPB flight changed at their site and that the life cycle shifted to bivoltine. No historical information on MPB attacks or voltinism is available for the Niwot Ridge site, although studies elsewhere at similar elevations reported a mix of univoltine and semivoltine broods (Amman 1973; Bentz et al. 2014). Adults were first caught in pheromone traps at the Niwot Ridge site on June 17, 2009, and June 21, 2010, and traps last caught adult beetles on September 20, 2009, and October 4, 2010. Sampling conducted in September 2009 on trees that were attacked in June 2009 showed signs of larval galleries, larvae, pupae, and some empty pupal chambers (suggesting that emergence had already taken place from the tree). A similar pattern was seen in 2010. None of the attacked trees were followed for more than a single year, and the proportion of univoltine and semivoltine brood at the site was therefore unknown. From these observations, Mitton and Ferrenberg (2012) suggest that climate change caused an unprecedented summer generation in the MPB, whereby dispersing adults in June produced broods that emerged as adults in September of the same year. They go on to infer that adults dispersing in June came from a cohort of eggs oviposited the previous fall (i.e., a winter generation), thereby resulting in two generations in one year (i.e., bivoltinism). Using published data on MPB low temperature developmental thresholds and predictions from a temperature-driven, mechanistic MPB phenology model, we demonstrate constraints to bivoltinism at their field site and provide a more likely scenario for their observations.

Constraints to MPB Bivoltinism

As shown in previous studies (DeLeon et al. 1934; Reid 1962; Bentz et al. 2014), warm summers can allow a proportion of offspring from MPB that attack new trees in June to complete a generation by September or October of the same year. This phenomenon is not an unprecedented response to recent warming, as suggested by Mitton and Ferrenberg (2012), but a sporadically occurring outcome of warm summers and the presence of nonunivoltine adults (i.e., reemerged parent adults and semivoltine brood adults) that overwintered and are able to emerge in June rather than July or August. Most importantly, we argue that the apparent occurrence of a summer generation does not equate to bivoltinism in this species. For bivoltinism to occur at Niwot Ridge, adult broods that completed a summer generation between June 2009 and September 2009 must have emerged, attacked new trees, and initiated a new cohort of eggs. This cohort must have then completed a generation across winter and emerged to attack new trees by June 2010 (i.e., two generations in a single year). Mitton and Ferrenberg (2012) did not provide compelling evidence for a second generation across winter. They sampled life stages under the bark of random trees in May and June in 2009 and 2010 and observed larvae, pupae, and teneral adults, although the timing of cohort initiation in these trees was not known. They presumed that these trees were attacked the previous fall (i.e., September 2009), thereby suggesting that MPBs could complete a second generation between September and June (i.e., a bivoltine generation; fig. 1). A key piece of missing evidence in the Mitton and Ferrenberg (2012) study is knowledge of when these trees were actually attacked. As described previously, overlapping MPB cohorts with varying life-cycle timing are common at high-elevation sites.

Without accurate observations on attack timing and brood emergence, we can use well-documented data on MPB low-development thresholds and thermal requirements and daily temperature data from a weather station at the Niwot Ridge Long-Term Ecological Research site (Niwot Ridge Long-Term Ecological Research, University of Colorado Mountain Research Station). These weather data, also used by Mitton and Ferrenberg (2012), allow us to evaluate the potential for completion of a winter

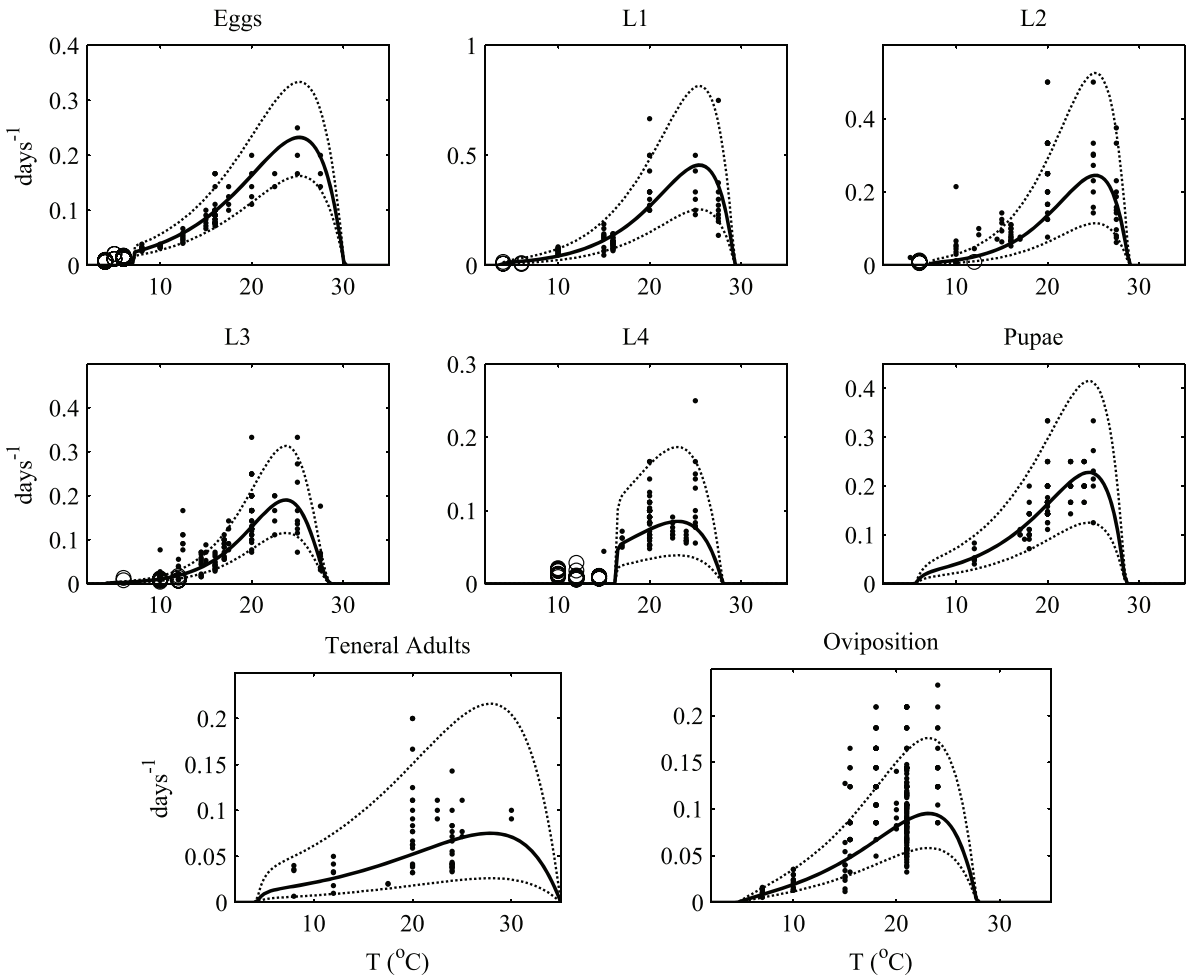

Figure 2: Mountain pine beetle development rate (1/development time in days to complete the life stage) data and estimated curves for seven life stages (eggs, instar 1 [L1], instar 2 [L2], instar 3 [L3], instar 4 [L4], pupae, and teneral adults) and oviposition. Shown are observed developmental rates (dots) across a range of temperatures (°C). Also shown are individuals that did not complete development (circles) during the duration of an experiment, with the maximum possible rate allowing noncompletion indicated. Data on temperatures that result in incomplete development highlight low temperature thresholds for development in each life stage. Bold solid curves are rates of development estimated using maximum likelihood. Parameters and functional forms are taken from Régnière et al. (2012). Dashed curves indicate predicted rates of development for individuals $\pm 2\sigma$ (lognormal) from the mean. Data underlying figure 2 are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.qt2qb (Bentz and Powell 2014).

generation between September and the following June at the Niwot Ridge site. Although eggs and early instars of MPBs have lower temperature thresholds that allow for development at relatively cool temperatures, fourth-instar larvae require temperatures approaching 17°C to become pupae (Safranyik and Whitney 1985; Bentz et al. 1991; Régnière et al. 2012; fig. 2). This high threshold for pupation directly controls seasonality and also reduces the chance that cold-sensitive life stages (i.e., eggs and pupae) will be present during winter (Logan and Bentz 1999). At the Niwot Ridge site, a cohort oviposited in September 2009 would not have received temperatures approaching 17°C until late May 2010 (fig. 1), leaving insufficient development time for completion of a generation by early June. Moreover, only 236 degree days (DDs) >5.5°C were accumulated between September 15, 2009, and June 15, 2010, which is insufficient thermal heat for completion of an MPB generation. To complete an MPB generation, more than 833 DDs >5.5°C are required (Carroll et al. 2004).

Mitton and Ferrenberg (2012) hypothesized that selection may have occurred in populations at their high-elevation site, thereby allowing their population to develop faster than populations previously studied at lower ele-

vations. At a 2,900-m site in California, Bentz et al. (2014) found that MPBs at high elevations can complete a generation with fewer DDs >15°C than populations at lower elevations. The time required to accumulate the required heat, however, can be greater compared with that of populations at lower elevations. Additionally, more than three times the thermal energy was required for a generation at the high-elevation site in Bentz et al. (2014; 70 DDs >15°C) relative to that accumulated at Niwot Ridge between September 2009 and June 2010 (22 DDs >15°C). This suggests that even if selection is occurring at high elevations, thermal energy at the site of Mitton and Ferrenberg (2012) was well below the known amount required for this insect to complete a generation, even compared with other high-elevation sites. In addition, any eggs deposited in September 2009 that did not eclose to a first instar rapidly would have been killed when temperatures dropped below the −17°C threshold for cold-induced egg mortality (Reid and Gates 1970; fig. 1).

Field data from other recently published studies tracking individual attacked trees also suggest that completing a winter generation between September and June is unlikely for MPBs. At a warm site in Washington, Lester and Irwin (2012) followed trees attacked between August 25 and September 20 and did not observe egg eclosion and first-instar larvae until July 22. At a warm site in southern California, Bentz et al. (2014) observed a summer generation and followed trees attacked in September and October through the end of the life cycle. Adults from eggs oviposited in September and October 2009 did not emerge from brood trees until July 2010, setting the phenological pathway back to univoltinism following a summer generation. Therefore, although a few MPBs can complete a summer generation in warm years, evolved thermal thresholds constrain a winter generation between September and June, limiting the potential for bivoltinism (fig. 1).

MPB Voltinism Predicted by a Phenology Model

A model developed to predict MPB phenology based on the physiological processes described above provides an additional tool for evaluating the potential for bivoltinism. Initially developed by Bentz et al. (1991), the model was parameterized with development time data for MPB life stages derived from constant-temperature laboratory experiments and was recently modified to include lognormal genetic variability of development times among individuals and accurate low- and high-temperature development thresholds (Gilbert et al. 2004; Régnière et al. 2012; fig. 2).

Mechanistically, the model predicts the probability that an individual in life stage j will complete development in a given time interval, taking as input the life stage's rate curve ($r_j(T)$; see fig. 2), lognormal genetic variance (σ_j^2), and current hourly phloem temperature (T). The total potential developmental index (R_j) is calculated by integrating phloem temperatures since the first attack ($t = 0$) through the rate curve,

$$R_j(t) = \int_0^t r_j(T(\tau))d\tau.$$

The probability that an individual starting at time t' can complete the stage by time t is computed using the lognormal distribution,

$$P_j(t|t') = \frac{r_j(T(t))}{\sqrt{2\pi\sigma_j^2 R_j^2(t)/R_j^2(t')}} \times \exp\left\{-\frac{[\log(R_j(t)) - \log(R_j(t')) + (1/2)\sigma_j^2]^2}{2\sigma_j^2}\right\}.$$

The distribution of emergence times in a given stage can be predicted on the basis of the emergence distribution from the previous stage; the input distribution of attacks on a tree serves as the initial condition. More details on this "cohort" approach to predicting the timing of life history and justification for the generality of a lognormal model for inherent genetic developmental differences in a population appear in Régnière and Powell (2013).

Mortality due to factors such as cold (Régnière and Bentz 2007) are currently not included in the phenology model. The model is driven by hourly temperatures and has been successfully used to predict MPB-caused tree mortality using observed temperatures (Powell and Bentz 2009, 2014). Hourly phloem temperatures appropriate for daily maximum and minimum air temperatures from the Niwot Ridge weather station (see above) were generated with the reverse-bootstrapping technique recommended by Lewis (2011) and tested in diverse landscapes by Powell and Bentz (2014). This technique uses an archive of air temperatures associated with phloem temperatures of MPB-infested trees. Daily phloem temperatures contemporaneous with the closest matching daily air temperatures to Niwot Ridge were inputted into the phenology model to predict MPB life-cycle timing and voltinism at the study site of Mitton and Ferrenberg (2012) between June 17, 2009, and December 30, 2011.

Mitton and Ferrenberg (2012) observed that trees attacked in June 2009 produced adults by September 2009. They inferred that these adults produced a second generation between September 2009 and June 2010. When initiated with a pulse of attacking adults beginning on June 8, 2009 (a week prior to the date of the first trap catch observed by Mitton and Ferrenberg [2012]), our model predicts that the majority of individuals would develop on

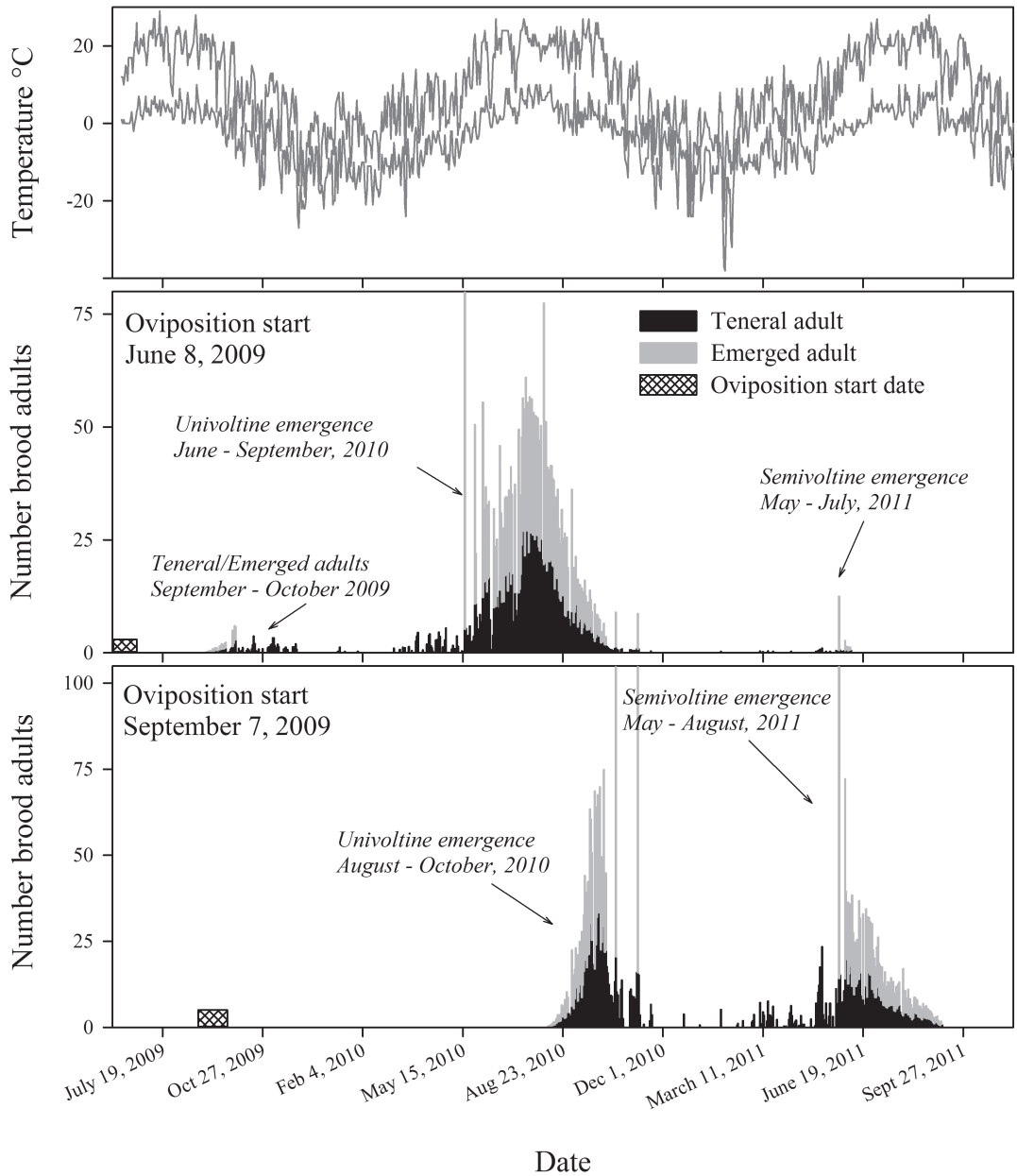

Figure 3: Daily maximum and minimum temperatures at the Niwot Ridge site (*top panel*). Phloem temperatures estimated from these data were used as input to the mountain pine beetle (MPB) phenology model using two attack dates, June 8, 2009 (*middle panel*), and September 7, 2009 (*bottom panel*). Shown is the predicted timing of the teneral adult stage and their emergence from trees following a period of maturation and temperatures >17°C. When oviposition is initiated on June 8, 2009, the majority of individuals are predicted to have emerged on a univoltine life cycle during the summer of 2010, with a small number emerging on a semivoltine life cycle in 2011. A few individuals were predicted to develop to the teneral adult stage in September 2009, consistent with the observations of Mitton and Ferrenberg (2012), although temperatures at the site were below the 17°C emergence threshold, and few individuals were predicted to emerge and attack new host trees. When oviposition is initiated on September 7, 2009, the model predicts a mix of univoltine and semivoltine emergence in 2010 and 2011, respectively. For a bivoltine life cycle to occur, eggs oviposited in September 2009 must have emerged by early June 2010. The model predicts that no individuals would have emerged prior to the middle of August 2010, thereby negating the possibility of a bivoltine life cycle at the Niwot Ridge site. Note that the phenology model does not include mortality due to cold. Sharp spikes in emergence are predicted to occur when teneral adults overwinter and temperatures first exceed the 17°C emergence threshold in spring.

a univoltine life cycle, emerging between early June and late September 2010, peaking in August 2010 (fig. 3). A small number of individuals would require an additional year, emerging in 2011. The model also predicts that a small number of individuals would complete development to the teneral and emerged adult stage by late September 2009 (fig. 3), consistent with what Mitton and Ferrenberg (2012) observed. Temperatures at the site during this time, however, were at or below the 17°C flight threshold for adult emergence (Safranyik and Carroll 2006; Bentz et al. 2014; fig. 3), so few adults were predicted to emerge. If we relax this constraint, however, and assume that adults did emerge and attack new trees in September, we can use the phenology model to evaluate whether a cohort initiated in September could complete a winter generation by the following June at Niwot Ridge, as suggested by Mitton and Ferrenberg (2012).

We initiated the model with a pulse of attacking adults that started oviposition on September 7, 2009, close to the date described in Mitton and Ferrenberg (2012) for a fall trap capture. Model predictions suggest that these attacks would result in a mix of univoltine and semivoltine broods that emerge in late summer 2010 and early summer 2011, not early summer 2010, as suggested by Mitton and Ferrenberg (2012; fig. 3). Our model predictions therefore provide additional verification that an MPB generation could not have been completed between September and June at the Niwot Ridge site and that the bivoltinism hypothesized by Mitton and Ferrenberg (2012) would have been physiologically impossible. These model results also suggest that the teneral adults observed by Mitton and Ferrenberg (2012) in May and June most likely came from a cohort initiated the previous June, not the previous September (fig. 3). The predicted emergence of MPB broods from trees attacked in September 2009 overlap with broods from trees attacked in June 2009, further highlighting the potential for overlapping cohorts at high-elevation sites.

Conclusions

Cohort splitting is common in the MPB due to genetic variation in thermal requirements and microclimatic variation among and within trees. As a result, a mix of semivoltine and unvioltine life cycles can be found during warm years at high-elevation sites (Bentz et al. 2014). Due to the mix of cohorts that could come from different generations and initiated on different dates, ascertaining the identity of a particular MPB cohort in the field requires following individual trees from the time they were infested, a key missing step in Mitton and Ferrenberg (2012). Although an MPB generation can be completed in a single summer in warm years (Hopkins 1909; DeLeon et al. 1934; Reid 1962; Mitton and Ferrenberg 2012), a second generation that occurs across winter would be necessary to achieve bivoltinism. Occurrence of this second generation is limited by evolved traits, including a high thermal threshold for pupation, that serve to maintain an appropriate seasonality. Instead of initiating bivoltinism, summer generations are followed by a life cycle that results in a return to either a univoltine or a semivoltine life cycle (Bentz et al. 2014; fig. 3).

Previous modeling studies using climate change scenarios have shown that univoltine and semivoltine life cycles in the MPB can produce a stable seasonality and that, given sufficient heat, bivoltine life cycles can also be stable (Jenkins et al. 2001; Powell and Logan 2005). Habitats with the thermal energy required for stable bivoltinism, however, are currently unknown within the distribution of the MPB (Bentz et al. 2014). Daily temperatures from Niwot Ridge, knowledge of MPB thermal thresholds, and predictions from an MPB phenology model confirm that the study site of Mitton and Ferrenberg (2012) did not have the thermal energy to produce a bivoltine life cycle. Observations of apparent bivoltinism in the MPB should be carefully considered given the ecological and economic impact of this insect. Increased understanding of thermal regimes and adaptations in life-history traits that would allow the MPB to surpass the physiological barrier that currently limits bivoltinism is needed. Climate change is already influencing range expansion into habitats previously too cool for the MPB, and this knowledge would contribute to our ability to predict potential MPB range expansion into habitats that are currently too warm.

Acknowledgments

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