

# Field Studies Demonstrate Bivoltinism in the Mountain Pine Beetle

(A Reply to Bentz and Powell)

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We appreciate Bentz and Powell's (hereafter interchangeable with "the authors") interest in our paper "*Mountain pine beetle develops an unprecedented summer generation in response to climate warming*". We are pleased the authors have confirmed the summer generation of mountain pine beetles (MPBs, *Dendroctonus ponderosae*) that we reported is now a widespread phenomena arising in response to greater than average annual temperatures. A recent paper by Bentz et al. (2013) also reported a switch from one to two generations of MPBs in roughly one year in a California site indicating that "bivoltinism" or two MPB generations in a year was not isolated to our Colorado sites. While Bentz et al. (2013) documented two generations within 13 months and state that technically the two generations must occur in 12 months to meet the definition of bivoltine, this switch to multiple generations of MPBs within the same time span historically necessary for one generation has large demographic implications. This decrease in

generation times is possible because, as reported by Bentz et al. (2013) “substantial genetic variation in development time is known to exist among MPB (*Dendroctonus ponderosae*) populations across the western United States.”

Despite their confirmation of summer generations of MPBs and the additional verification that a summer generations can produce offspring that emerge and mate during the same season, Bentz and Powell argue against our report of bivoltinism. The authors' arguments fall into three categories: (1) critiques of our methodology which the authors consider inadequate for monitoring MPB development—*i.e.*, while they support our report of a summer generation, they argue that we did not demonstrate bivoltinism because of flaws in our experimental design; (2) arguments that beetles in our study sites cannot exhibit bivoltinism because this would counter the authors' assertion that generation times of MPBs are relatively similar across their expansive range; and (3) conflicts between the authors' computer simulation-model of MPB phenology which suggests MPBs require at least one year per generation and our direct field-observation of two generations of MPBs in one year.

We reject these criticisms because: (1) Bentz and Powell misrepresent our study's methodology and subsequently take issue with their version of our methods and not those we employed; (2) MPB development rates and generation times are documented to be highly variable, even under equivalent thermal regimes, such that beetles living in shared environments and from the same broods can have generation times differing by more than two-fold (Reid 1962, Bracewell et al. 2013, Bentz et al. 2013); and (3) given that the thermal energy needed by MPBs to develop from egg to adult within and among broods is highly variable (Bentz et al. 2001 & 2013, Carrol et al. 2006, Bracewell et al. 2013), the application of one phenology model to all MPB populations regardless of location or environment is questionable. In fact, the derivation of

one phenology model which would be accurate for all beetles within a population, let alone across all populations of MPBs is highly improbable given the evidence of genetic differentiation among MPB populations (Stock and Amman 1980, Kelley et al. 2000, Bracewell et al. 2011, Gayathri-Samarasekera et al. 2012); the importance of local adaptation by MPB populations to thermal regimes across latitude and elevation (Bentz et al. 2001, Bracewell et al. 2013); and the documented effects of local ecological influence such as host tree species and quality on beetle growth and development (Sturgeon and Mitton 1986; Langor 1989; Langor et al. 1990; Cerezke 1995). While we will expand in detail below, we assert that the model used by Bentz and Powell—which was parameterized using data on MPB development in Petri dishes at constant temperatures in a laboratory—is not likely to capture the full range of variation in phenotypes and responses to the range of conditions found in natural field settings (for model development see Logan and Amman 1986, Bentz et al. 1991, Gilbert et al. 2004). Thus, using this model to reinterpret our findings and dismiss our first-hand observations is unfounded.

### **Comments on Our Methods and Description of MPB Life History**

Bentz and Powell strongly critique of our methods for assigning MPBs to cohorts and for following MPB development. In particular, the authors argue that flaws in our procedure led us to monitor broods with unknown dates of inception, and that by using random trees we lacked sufficient knowledge of MPB attack history leading to a scenario where we misidentified adult beetles from prior attacks as recently eclosed (emerged from pupation) beetles, or as stated by Bentz and Powell:

“(Mitton and Ferrenberg) sampled lifestages under the bark of random trees... the timing of cohort initiation in these trees was not known. They presumed these trees were attacked the previous fall (i.e., September 2009)...a key piece of missing

evidence in the Mitton and Ferrenberg (2012) study is knowledge of when these trees were actually attacked.”

Given this presumed flaw, the authors argue for the dismissal of our observations of beetle development and instead resort to the application of their phenology simulation model to determine if beetles in our field sites could produce multiple generations in a year.

We reject this criticism and encourage the authors to read paragraphs three and four of our methods where we explain our procedures for selecting trees with no prior MPB attacks, and hence no existing broods under the bark. Using trees with no pre-established broods, we then used pheromone lures to attract MPBs to pre-determined target trees and subsequently examined each tree for attacks on a regular time interval in order to establish reasonable estimates of attack dates and locations within a tree.

Trees attacked in June 2009 released adult beetles in August 2009, and we noted that previously unattacked trees came under attack at the same time. In June 2010, exit holes appeared on trees first attacked the previous summer in August. We peeled the bark and found that the brood inside was in various stages of development, including larvae, empty pupal chambers, teneral adults and numerous fully pigmented adults boring exit holes (Figure 1). These observations revealed the existence of a summer generation, and also that some beetles completed development between August 2009 and June 2010, demonstrating the existence of a winter generation.

Because Bentz and Powell support our report of a summer generation in our Colorado field sites in 2009, but subsequently argue the impossibility of a winter generation, we calculated growing degree days (GDDs) available for development of the summer MPB generation in 2009, and compared that value with the GDDs available for the winter MPB generation which released

adults in June of 2010. We calculated GDDs by subtracting the previously reported MPB developmental threshold of 5.5°C from daily mean temperatures (long term data available from the Niwot Ridge LTER C-1 climate station, [niwot.colorado.edu](http://niwot.colorado.edu); data and calculations analyzed here available from Ferrenberg 2014, Dryad Digital Repository: [doi:10.5061/dryad.4df03](https://doi.org/10.5061/dryad.4df03)) and then transforming negative values to 0 before summation as in Mitton and Ferrenberg (2012). From June 8 (the date we reported seeing the first MPB attacks) to August 15, 2009 (the date when we first noted emergence of a summer generation) the summer generation had 391 GDDs to complete development. The following winter generation, which we consider as beetles developing from August 16, 2009 to June 27, 2010 (the date we noted the first MPB attacks on trees in 2010) had 379 GDDs. Thus, the numbers of GDDs available for the summer and winter generations differed by only 12 GDDs, which is equivalent to one calendar day with a mean temperature of 17.5°C.

We also reject Bentz and Powell's use of data recorded > 550 km away from our study site for characterizing historical MPB life history of our study's location (Bentz et al. 2013). As reported in our original note, a report from a U.S. Forest Service experimental forest site at a similar elevation and only 30 km west of our study site verifies that MPBs attacking a shared tree species had univoltine generations in years prior to our study (Tishmack et al. 2005). Thus, we reiterate that broods observed for our study had a mixture of univoltine (which we consider historically common) and bivoltine (which we observed arising in response to warming) generations.

## **Documented Variation in MPB Responses to Temperature**

A decrease in MPB generation times in response to warming is possible because of genetic variation for development rates within and among populations (Reid 1962, Reid and Gates 1970, Bentz et al. 2001, Bracewell et al. 2013, Bentz et al. 2013). In fact, Bentz and Powell note in their comment that sufficient variation exists in the development rates of MPB populations to allow some high elevation populations to exhibit “a mix of univoltinism (one generation per year) and semivoltinism (one generation every two years)” within the same thermal regime. Furthermore, median generation times across broods monitored by Bentz et al. (2013) varied by more than six-fold (mean = 373 days, range = 585 days) while nearly 39% of broods exhibited a mixture of voltinism strategies indicating that even sibling beetles in a shared environment can vastly differ in the time and associated thermal energy necessary for completing development. Importantly, patterns of development time exhibit adaptive variation; the thermal energy required for one generation is less in sites at higher elevation and latitude (cooler climate) than in sites at lower elevation and latitude (warmer climate) (Bracewell et al. 2013, Bentz et al. 2013).

It is paradoxical that Bentz and Powell assert “a minimum of 883 degree days (GDDs > 5.5 °C) is needed to complete development”, and then use this assertion to reject our report of bivoltinism in a MPB population. The authors (and colleagues) have previously reported a nearly three-fold variation in the number of degree days (GDDs > 10.0°C) required for MPB development across studies (Carroll et al. 2006), while also reporting that total degree days (GDDs > 15°C) necessary for emergence across field populations varied by nearly seven-fold (Bentz et al. 2013). This evidence of heritable genetic variation for development and growth rates indicates that either the threshold temperature for development, or rates of development and growth (or any combination) are variables subject to selection to adapt populations to their local

environments and changing climate. Evidence for climate-driven changes in life history, particularly generation times, have been reported in other MPB populations and other *Dendroctonus* beetles. For example, MPBs in the Greater Yellowstone ecosystem are shifting from a semivoltine (one generation every two or more years) to a univoltine life cycle (Logan et al. 2010), while some populations of spruce beetles (*D. rufipennis*) have decreased generation times from two years to one (Berg et al. 2006). The reproductive advantage of shorter generation times would create strong selection favoring phenotypes capable of rapid growth and development.

## **Conclusion**

Bentz and Powell confirmed our observation of a summer generation of MPBs in 2009, but argued that eggs deposited in August 2009 could not complete development by June 2010. However, broods we observed as being established in August 2009, at the same time the summer generation was emerging, released adults the following summer in June, 2010 (see Figure 1 in Mitton and Ferrenberg 2012). The author's criticisms of our methods for following beetle development are unfounded as they ignored our reported procedures and later argue for a future study using methods nearly equivalent to those we employed. Although Bentz and Powell's simulation model denies the possibility of bivoltinism, we show that the growing degree days (GDDs) available for the summer generation of MPBs in our field site (which is accepted by the authors as a valid generation) is nearly equivalent to the GDDs available for the winter generation we observed. Thus, reinterpreting our findings via the application of the authors' phenology model which is based on MPB development in Petri dishes under constant temperatures in a laboratory is neither necessary, nor founded given that several studies confirm

the existence of substantial heritable variation in MPB development rates, even for siblings developing in equivalent environments and thermal regimes.

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## Figure legend

Figure 1. A characteristic mountain pine beetle (*Dendroctonus ponderosae*) gallery established in the month of August, releasing mature beetles the following June. After approximately 360 growing degree days (GDD), the brood consisted of larvae, teneral adults and mature adults chewing exit holes. Empty pupal chambers and exit holes indicate that some beetles have already emerged.