

Effect of Spring and Winter Temperatures on Winter Moth (Geometridae: Lepidoptera) Larval Eclosion in the Northeastern United States

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ABSTRACT Field and laboratory experiments were conducted to elucidate various factors influencing the temperature-dependent larval eclosion of winter moth, *Operophtera brumata* L, in New England. We found no difference in duration of the embryonic stage of eggs reared from larvae collected in Massachusetts (MA) and on Vancouver Island, British Columbia (BC), where winter temperatures are rarely below freezing. The number of growing degree days (GDD) required for larval eclosion declined with the number of days chilled in the laboratory and number of days below freezing in the field, confirming the findings of previous studies. Thus, eggs hatched with fewer GDD, when the spring came later than usual. Date of oviposition had no effect on date of hatch. Eggs laid by naturally occurring (feral) females hatched sooner, with lower GDD, than eggs from laboratory-reared females from MA and BC held on the same trees over the winter. South-facing eggs on the stems of trees hatched on average 1.6 days sooner than north-facing eggs. GDD calculated from bihourly measures of temperature were 15% greater than GDD estimates based on the average of daily maximum and minimum temperatures, as used by many GDD estimates made for online sources. Over two years, the mean GDD in °C for hatch of feral eggs was 176.53 ± 6.35 SE based on bihourly temperature measurements, a 1 January start date, and a 3.9°C developmental threshold. This value varied markedly, however, between the two years.

KEY WORDS growing degree days, phenology, temperature dependence, bud burst synchrony, hatch time

Growing degree days (GDD) are widely used in agriculture (Coop 2010) to predict phenological events such as flowering time or crop maturity. Entomologists use the term to predict emergence or eclosion of various insect species. Estimation of GDD assumes that rate of development, given by the inverse of the number of days to complete development, is a linear function of temperature (Logan et al. 1976). In fact, this function is almost never linear, and various nonlinear models have been proposed (Logan et al. 1976). However, in the midrange of temperatures between maximum and minimum temperature threshold, the rate is usually close to linear and, consequently, estimating development or spring emergence using GDD can be quite accurate (Curry and Feldman 1987).

This study was designed to explore the hatch phenology of the winter moth (*Operophtera brumata* L.), an introduced forest pest from Europe. It is a major defoliator of a wide range of deciduous trees and shrubs (Wint 1983), including oak (*Quercus*), maple (*Acer*), apple (*Malus*), and blueberry (*Vaccinium*). In North America, it was first detected in Nova Scotia in the 1930s and has since spread to the Pacific Northwest and to New England (Roland and Embree 1995, Elkinton et al. 2010). Populations in Nova Scotia and

the Pacific Northwest have been successfully controlled by a tachinid parasitoid from Europe, *Cyzenis albicans* Fallen (Roland and Embree 1995), and efforts are underway to introduce this fly into the northeastern United States. To ensure success of the biocontrol agent, the parasitic flies must be allowed to emerge and, subsequently, be released during a small window of days following winter moth larval eclosion. Furthermore, various investigators have used GDD estimates to predict the degree of synchrony between larval eclosion and bud burst on host trees (Visser and Holleman 2001). This synchrony has been shown to play a key role in causing changes in winter moth population density (Embree 1965, Varley and Gradwell 1968, Jepsen et al. 2009).

Timing of winter moth larval eclosion has been studied in Nova Scotia, Canada (Embree 1970), Oregon, USA (Kimberling and Miller 1988), Scotland, United Kingdom (Watt and McFarlane 1991), Norway (Peterson and Nilssen 1998), and the Netherlands (Visser and Holleman 2001). All have found that temperature plays a major role in developmental time of eggs. Embree (1970) developed a GDD model for winter moth larval eclosion. He reported a developmental temperature threshold of 3.9°C and determined that hatch occurred when GDD reached 192°C from a start date of 1 April, which in Nova Scotia was about 6 wk before the winter moth larvae eclosed.

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Wylie (1960) studied the effect of temperature on the duration of the embryonic stage of winter moths collected from different European locations. He observed that the duration of embryonic stage is only 2 mo in southern Italy, but nearly 8 mo in northern Europe. Wylie showed that differences in egg duration were based on temperature, as well as intrinsic differences between winter moth populations. Wylie tested eggs of winter moths from Versailles, France, and Oldenburg, Germany. When eggs from these locations were reared at the same temperature, he found differences in the duration of egg stage, which suggested that the duration was affected by intrinsic factors. Wylie (1960) also showed that increasingly low temperatures below the threshold do not have significant effect on the duration of egg stage. Egg duration was relatively the same for eggs held at -4.5°C , -12°C , and -16°C for equal amounts of time. Various studies of winter moth in Oregon (Kimberling and Miller 1988), Scotland (Watt and McFarlane 1991), and the Netherlands (Visser and Holleman 2001) showed that the GDD accumulated when winter moth hatch declines as the number of "frost" days (defined as days with minimum temperatures below 0°C from 1 December onwards) in the winter and early spring increases. Visser and Holleman (2001) further showed that the earlier hatch of winter moths in recent years due to global climate change has desynchronized winter moth with oak (*Quercus*) bud burst, its favored host species, and caused a host shift to other species.

The current study explored the effects of spring and winter temperatures on the duration of the winter moth egg stage and the date of hatch in New England. We used laboratory and field experiments to compare eggs reared from larvae collected in Massachusetts and British Columbia, as well as the hatch of eggs laid in the field by naturally occurring (feral) females in Massachusetts. Predicting larval eclosion of the winter moth in the northeastern United States would be a valuable tool to determine when to apply pesticides and also to synchronize the release of bio-control agents. It would help researchers estimate the synchrony of winter moth hatch with host tree budburst, which varies from year to year and plays a vital role in the population dynamics of the winter moth system (Embree 1965, Jepsen et al. 2009, Varley and Gradwell 1968).

Several possible growing degree day models for predicting hatch were evaluated. These included a constant GDD model and models in which GDD declines as either a linear or exponential function of the number of days when eggs are held at temperatures below 0°C . The effects on GDD estimates were also examined by varying the start day of temperature observations. Additionally, estimates from our field temperature recorders were compared with two online GDD calculators.

Materials and Methods

Source of Eggs. Several thousand winter moth larvae were collected from locations in Massachusetts (MA) and Victoria, British Columbia (BC), in the spring of 2011 and 2012. Larvae were reared on foliage

in large plastic buckets with a 1-cm layer of peat moss in the bottom of the bucket. Larvae dropped from the foliage into the peat moss where they pupated in late May or early June. Pupae were held in ventilated 30-cm-diameter petri dishes in two 16°C growth chambers (photoperiod of 16:8 [L:D] h) from June to November. Each petri dish contained ~ 300 pupae placed on filter paper over a moistened layer of sand and they were misted with water weekly to keep the pupae from drying out. The water contained 1% sodium propionate to prevent mold from growing on the pupae. In November, the temperature in both chambers was dropped to 10°C , and dropped again to 7°C 10 d later to induce adult emergence. Several hundred adults were mated in groups of about 10 males and 10 females in 18- by 10-cm mesh bags. After the eggs were laid, they were loosely shaken off the bags and stored at 7°C for no longer than 10 d until used in the experiments described below.

Laboratory Studies. Eggs used in this study were laid within a 6-d period (between 6 and 12 December 2011). Egg embryonation was determined when the eggs turned from green to pink. Embryonated eggs were then collected from the mesh bags with a fine tip, sterilized paint brush and transferred in groups of 30 to small Petri dishes. The dishes were lined with filter paper which was slightly moistened with distilled water. Eight egg-chill groups were set up for eggs from each source locality (MA or BC) with 30 eggs per dish. Once embryonation was complete, all dishes were moved into a growth chamber, where they were held at 1°C for 0, 14, 28, 42, 56, 70, 84, or 98 d. The photoperiod in this chamber was set to 8:16 (L:D) h to simulate winter photoperiod. After that, dishes with eggs were moved to other growth chambers for rearing at 5, 10, 15, 20, or 25°C with a photoperiod of 16:8 (L:D) h. One dish of 30 eggs was reared at each temperature for each of the chill day treatments, until the eggs all hatched. Eggs were checked daily and hatch was recorded.

To determine the developmental threshold temperature T_{th} and GDD for the individual groups, days to hatch were plotted against the rearing temperatures of 5, 10, 15, 20, and 25°C , and data were fit to linear regression lines. The values at 25°C were excluded because most eggs failed to emerge at this temperature. To estimate the GDD and developmental threshold the following equations were used:

$$GDD = \frac{1}{b}, \quad T_{th} = -\frac{a}{b} \quad (1)$$

where a is the intercept and b is the slope of the linear regression (Curry and Feldman 1987). GDD calculated in this manner were plotted against the number of days in chill, and both linear and exponential regression lines were fit to this data.

Field Studies. Separate groups of 50 eggs from MA and BC were counted and stuck to a piece of labeling tape. The tape with eggs was then placed into a 4- by 5-cm fine mesh bag and deployed in the field on 28 November 2011 and 19 November 2012. At six

sites in eastern Massachusetts, two bags each of MA and BC eggs were attached with staples at a height of 1.5 m to the north and south side of the stem of a randomly selected red or black oak (*Quercus rubra* or *Q. velutina*). The sites were selected to span the region infested with high densities of winter moths and included some that were close to the ocean on Cape Cod (Yarmouth, 41° 41'11.06" N, 70° 17'15.36" W and Falmouth 41° 37'34.89" N, 70° 34'49.66" W). The other sites chosen were 30–40 km inland where we might expect colder winter temperatures (Hanson 42° 3'39.88" N, 70° 50'38.59" W; Hingham 41° 13'0.57" N, 70° 51'55.92" W; W. Bridgewater 42° 1'15.55" N, 70° 58'58.42" W; and Wellesley 42° 18'31.18" N, 71° 16'0.59" W). Accompanying the egg bags on the north and south side of each tree was an additional mesh bag containing a Thermochron iButton (DS1921G, Dallas Semiconductor Corp, Dallas, TX) data logging device to record bihourly temperatures. On each tree, a group of 100 feral eggs was identified on the north and south facing sides, and marked on the adjacent bark with paint. This was not done on some trees, especially in 2012 when densities of feral eggs were too low. Those eggs were also monitored for hatch.

To determine if the date of oviposition had an effect on the timing of hatch, three batches of eggs from MA were oviposited in the lab, and then deployed onto a tree in Yarmouth, MA, on three different dates. Egg groups were deployed on 19 November 2012, 4 December 2012, and 17 December 2012, and hatch was recorded the following spring. This experiment was designed to help explain differences in date of hatch between the lab-reared eggs of a known oviposition date (MA and BC) and feral eggs of an unknown oviposition date.

Estimating GDD. A simple GDD model was developed to estimate hatch over a developmental threshold temperature of 3.9°C (Embree 1970), using various start dates. We used 3.9°C instead of our own slightly lower value, in order to compare our findings with those of other researchers, as cited in Visser and Holleman (2001), all of whom used 3.9°C as a threshold temperature. Several methods were used to determine the GDD on the date of 50% hatch. The methods were based on the bihourly temperature recordings from iButtons made over the period between egg deployment and hatch, as well as GDD estimates obtained from online sources.

Bihourly temperature data were used from field-deployed iButtons to calculate degree days per day above the developmental threshold (3.9°C) and below a maximum temperature ($MaxT$) of 25°C. GDD was the accumulated sum of these daily degree days from a specific start date (1 January, 1 February, or 1 March) up to the date of 50% hatch [see equation 3.1 in Curry and Feldman (1987)].

$$\sum_{i=1}^n \sum_{j=1}^m \frac{T_{ij} - T_{th}}{m} \quad (2)$$

for all $T_{th} < (T_{ij}) < MaxT$. Here $T_{th} = 3.9^\circ\text{C}$ (Embree 1970), $m =$ number of samples per day (in our case

$m = 12$), $n =$ number of days, and the start date was typically 1 January (Visser and Holleman 2001) or other dates, as indicated below. $MaxT$ is the temperature above which no further increase in growth rate occurs with increasing temperature, as determined in our laboratory studies. In our system, $MaxT = 25^\circ\text{C}$, which was the maximum temperature at which egg development was observed in the laboratory. For bihourly temperatures for which $T_{ij} \leq T_{th}$, no bihourly fractional degree days were accumulated and for temperatures where $T_{ij} > MaxT$, the bihourly fractional degree days accumulated were $MaxT - T_{th}$. For the benefit of the many potential users of our findings, such as arborists and extension specialists in the United States, bihourly GDD in Fahrenheit were also calculated where $T_{th} = 40^\circ\text{F}$ and $MaxT = 70^\circ\text{F}$. When the developmental threshold temperature is the same, GDD $^\circ\text{F}$ equals (GDD $^\circ\text{C}) \times 9/5$. Here, we used $T_{th} = 40^\circ\text{F}$ instead of $T_{th} = 39^\circ\text{F}$, because that is a base temperature available for most online GDD estimators. Previous investigators of winter moth GDD have often used sine wave approximations (Baskerville and Emin 1969) to estimate the continuous diurnal record of temperature from daily maximum and minimum temperatures recorded at nearby weather stations (Embree 1970, Kimberling and Miller 1988, Visser and Holleman 2001). We used the same method to calculate GDD from the Web site www.uspest.org (Coop 2010).

Growing Degree Day Estimates From Daily Average of Maximum and Minimum Temperatures. Another objective was to compare our field estimates of GDD from our iButtons with the GDD estimates obtained from the Network for Environment and Weather Applications (NEWA) at Cornell University (NEWA.cornell.edu 2014, accessed 3 March 2015). Most extension professionals and arborists in New England who might use our findings currently obtain estimates of GDD from this site. Although these online estimates are derived from weather stations that were not at the exact location where our test eggs were observed, the temperature data collected were from the same town or a neighboring town. The Cornell site and many other extension Web sites in the United States calculate GDD from daily maximum and minimum temperatures:

$$GDD = \sum_{i=1}^n \frac{T_{i,max} - T_{i,min}}{2} - T_{th} \quad (3)$$

whenever $T_{th} < (T_{i,max} - T_{i,min})/2 < maxT$. Here T_{th} is the lower developmental threshold (in our case = 40°F or 3.9°C, (Embree 1970)), n is the number of days between 1 January or some other start day and the day of hatch, $T_{i,max}$ and $T_{i,min}$ are the respective maximum and minimum temperatures on day i , and $maxT$ is the upper developmental threshold (25°C or 70°F) above which there are no further increases in developmental rate. For days in which $(T_{i,max} - T_{i,min}) < T_{th}$, degree days accumulated on that day equal 0, and for days where $((T_{i,max} - T_{i,min})/2) > maxT$ the day degrees accumulated on that day is $MaxT - T_{th}$. In order to

compare our on-site estimates of GDD with those of the NEWA site, these same estimates of GDD were applied to the daily maximum and minimum temperatures recorded by our iButtons. These calculations are presented in Fahrenheit and were applied to the feral eggs, because these are the comparisons most relevant to the majority of users in the United States.

By testing a variety of start dates, we hoped to determine which start date would yield the most accurate GDD prediction of hatch. The first days of January, February, and March were chosen as start dates to calculate GDD. To compare the relative performance for calculating GDD, both with our iButtons and from the online sources, the mean deviation between the GDD estimates at each site from the overall mean of those estimates across all sites in both years was calculated. The rationale for using this as a measure of GDD performance was that the GDD estimate that best approximated both the physiological heat accumulation process within each egg and the actual heat accumulated by the eggs over the winter would minimize the variance or mean deviation of the value at each site from the overall mean of that estimate at all sites and years. For each field site, the GDD deviation at each site was converted to a positive number by taking the square root of $(\text{GDD} - \text{mean GDD})^2$. The average deviation in GDD was converted to days from degree days by dividing average GDD deviation by the mean number of degree days accumulated per day during the week when eggs were hatching. This value tells us the average number of days between the predicted and actual days of hatch.

Effect of Winter and Spring Cooling. Visser and Holleman (2001) summarized data on winter moth hatch from Scotland, Oregon, and their own data from the Netherlands to show that the GDD required for winter moth hatch declined with increasing numbers of “frost days,” defined as days when the minimum temperature is below 0°C from 1 December onwards. To compare our data with those presented by Visser and Holleman (2001), we also tabulated “frost days” with our iButtons and plotted GDD versus frost days alongside their data and plotted linear and exponential regression lines. Similar plots were made for our data from feral eggs for GDD in Fahrenheit.

Statistical Analyses. Paired t-tests (PROC MEANS, SAS 9.3, SAS Institute 2012) were used to test for differences in dates of hatch or GDD on the north and south sides of each tree or for comparisons of different estimates of GDD and deviations of GDD from the mean. An ANOVA (PROC GLM, SAS 9.3, SAS Institute 2012) coupled with Tukey’s studentized range procedure was used to test for differences in hatch dates between eggs reared from naturally occurring (feral) eggs and the laboratory-reared eggs that were deployed from MA or BC.

Results and Discussion

Laboratory Results. *Laboratory Estimates of GDD and Temperature Thresholds.* In our lab data, the developmental threshold was determined by fitting

a linear regression to plots (Fig. 1) of development rate ($1/(\text{days to hatch})$) versus rearing temperatures of 5, 10, 15, and 20°C for each of the groups held for different numbers of days at 1°C. The plots for the eggs from MA were very similar to those for the eggs from BC. The regression lines plotted in Fig. 1 show that the assumption of linearity embodied in the GDD calculation is reasonable for the data at these temperatures. Egg development occurred above a mean temperature threshold of $3.55^\circ\text{C} \pm 0.30$ SE for BC eggs and $3.67^\circ\text{C} \pm 0.31$ SE for MA eggs (Table 1). These estimates are quite close to the 3.9°C threshold estimated by Embree (1970).

The number of GDD above this developmental threshold decreased as the length of time held at 1°C increased (Fig. 2), reminiscent of the field data presented by Visser and Hollerman (2001). Both the BC and the MA eggs had virtually the same response. The effect appeared to reach a plateau after about 70 d, and the number of chill days (1°C) no longer had much effect on the GDD (Table 1, Fig. 2). For this reason, an exponential model ($R^2 = 0.902$) fit these data slightly better than a linear model ($R^2 = 0.825$, Table 2.). From a physiological standpoint, a declining exponential model is not surprising. If there were a hypothetical substance in the egg that prevented development and that decayed at a constant rate with time below a threshold temperature, the concentration of the substance, and thus its impact on GDD, would decline exponentially.

Field Results. *North vs. South-facing Eggs.* Eggs from all three sources (MA, BC, and feral) hatched about 3wk earlier in 2012 than in 2013 (Fig. 3A, B). South-facing eggs hatched on average 1.6 d earlier than north-facing eggs in both years ($t = 2.99$, $df = 27$, $P = 0.006$). By converting the data to GDD (Fig. 3C, D) most, but not all, of the differences between years disappeared. We surmised that by recording temperature with south-facing and north-facing iButtons, we would accurately record the GDD accumulated on each side. In other words, we expected the GDD estimates from the north-facing iButtons, when the north-facing eggs hatched, would be nearly equal the GDD that had accumulated on the south-facing iButtons, when south-facing eggs hatched a few days earlier. Such was not the case. South-facing iButtons recorded far more GDD when the eggs hatched on that side of the tree compared with the north-facing iButtons (Fig. 3C, D; $t = -3.44$, $df = 28$, $P = 0.002$). This can only mean that the south-facing iButtons accumulated more thermal units than did the winter moth eggs right beside them. Perhaps, because they are larger than the eggs and made out of metal, they absorbed more heat. The relevant literature on this topic (e.g., Bakken 1992) reveals that measuring or estimating the temperature of small insects exposed to sunlight, in contrast to air temperature, is not a simple matter. For this reason, we discarded the data collected by the south-facing iButtons in all subsequent analyses. Instead, we used the north-facing iButtons to estimate GDD for egg hatch on both the north and south side of each tree. Such

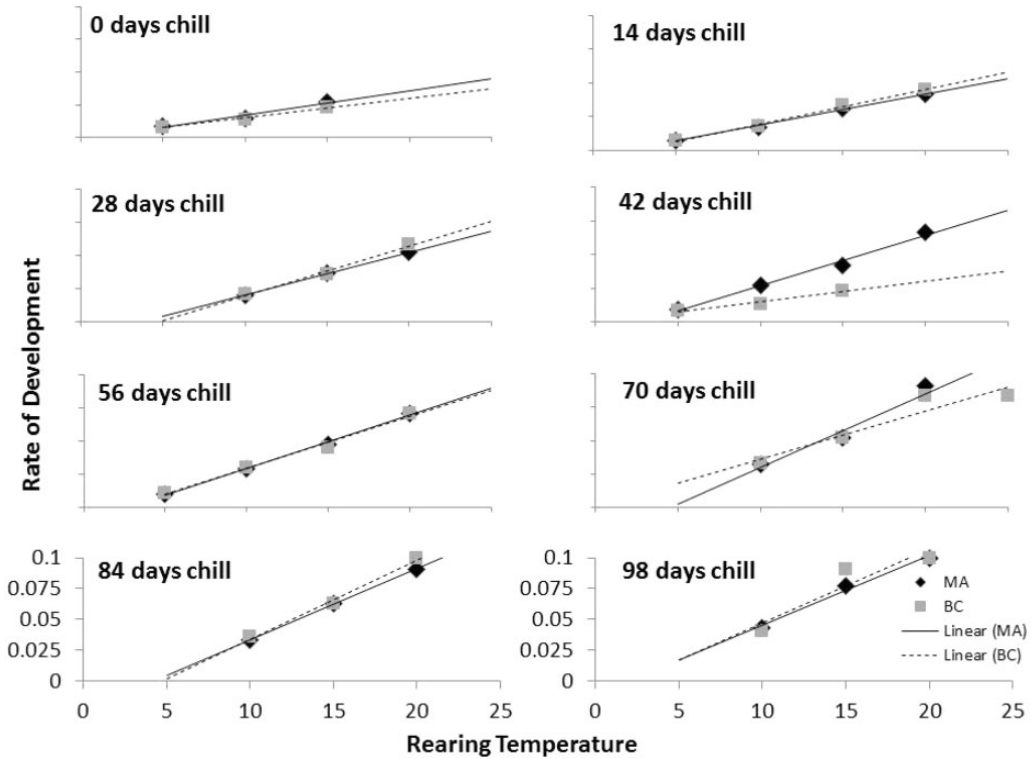


Fig. 1. Linear regressions of rate of development (1/number of days to 50% hatch) plotted versus rearing temperature in laboratory growth chambers for winter moth eggs laid by females reared from larvae collected from MA or BC and held for different numbers of days in chill (at 1°C) after oviposition before rearing at higher temperatures.

Table 1. Laboratory estimates of developmental threshold temperature and number of GDD required for hatch of eggs held at 1°C for different numbers of days

No. of days in chill	Developmental threshold temp Celsius		No. of GDD Celsius	
	MA	BC	MA	BC
0	3.96	3.16	400.00	526.32
14	2.75	3.29	416.67	357.14
28	3.63	4.66	312.50	263.16
42	4.31	3.58	238.10	250.00
56	3.21	3.07	238.10	243.90
70	4.98	3.72	169.49	200.00
84	4.16	4.75	172.41	156.25
98	2.33	2.17	175.44	166.67
Mean	3.67	3.55		
Std. Error	0.31	0.30		

Estimates are generated from linear regressions shown in Fig. 1. Eggs were oviposited by female winter moths collected as larvae from sites in MA or Vancouver Island in BC and then reared to the adult stage in growth chambers.

Developmental threshold temperature = $-1(a/b)$ from the linear regressions $R = a + bT$ where T is rearing temperature (°C) and R is the rate of development = $1/(\text{no. of days to hatch})$.

From the linear regressions shown in Fig. 1, $GDD = 1/b$

data are comparable with those collected by most other researchers and users, who collect data from weather stations with shaded temperature sensors. These include the weather stations generating data for the online GDD estimates.

Effects of Egg Source. Significant differences across both years were found, among the three egg types (MA, BC, and feral) both in hatch dates (Fig. 3A, B; $F = 7.17$, $df = 2, 29$, $P = 0.003$) and in GDD (Fig. 3C, D; $F = 6.52$, $df = 2, 30$, $P = 0.004$). There were, however, no significant differences in hatch dates (Fig. 3A, B) or GDD (Fig. 3C, D; Tukey's test, $\alpha = 0.05$) between eggs reared from larvae collected in BC or MA. This result was surprising, because previous studies (Wylie 1960, Visser and Holleman 2001) showed large differences in hatch times or GDD between winter moths collected from different locations. In both years, feral eggs on both the north and south sides of sample trees hatched several days earlier than the BC or MA eggs in mesh bags on the same trees (Fig. 3A, B; Tukey's test, $\alpha = 0.05$). We thought this difference might be due to differences in the date of oviposition. Winter moth males had been flying for a week or more before we deployed eggs in 2012 in the field study. To test this idea, eggs that were oviposited in the laboratory were deployed in the field on three different dates separated by 2 wk at one site (Table 3). These eggs hatched on virtually the same day the following spring, so it is clear that date of oviposition does not account for the differences between the feral eggs and the eggs hatching in mesh bags. The experiment also makes it clear that winter moth eggs accumulate little or no GDD in November and December, when

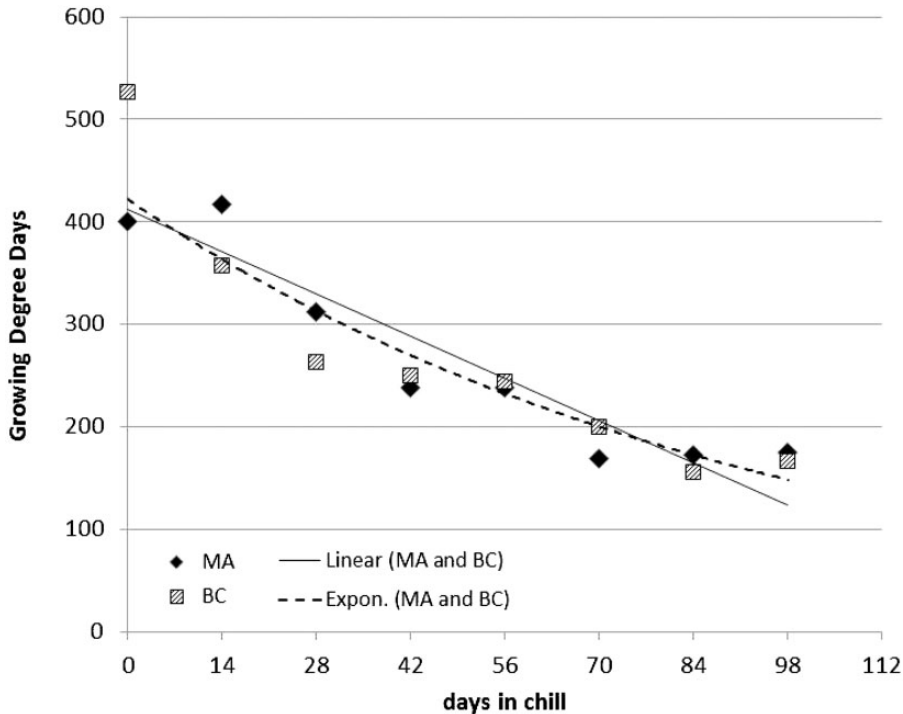


Fig. 2. Linear and exponential regressions of the GDD estimated as in Table 1 plotted versus number of days in chill for eggs from moths from MA and BC shown in Fig 1.

Table 2. Linear^a and exponential^b regression coefficients of GDD as a function of days in chill in the laboratory (Fig. 2) or days with temperatures < 0°C in the field in our own data and in studies from Oregon, Scotland, and the Netherlands, as presented in the Visser and Holleman (2001 see Fig 4)

Figure	Egg source	Year	°C or °F	Frost days	Model	Intercept	Slope/exponent	R ²	Pr > F
2	MA and BC lab	2012	C		Linear	412.46	-2.951	0.825	<.0001
2	MA and BC lab	2012	C		Exponential	421.83	-0.011	0.902	<.0001
4	Scotland	2001	C	<0°C	Linear	381.19	-2.8559	0.977	0.002
4	Oregon	2001	C	<0°C	Linear	442.2	-12.516	0.902	0.05
4	Netherlands	2001	C	<0°C	Linear	345.57	-1.417	0.866	0.007
4	BC field	2012/2013	C	<0°C	Linear	202.88	-0.288	0.029	0.451
4	MA field	2012/2013	C	<0°C	Linear	211.11	-0.374	0.057	0.285
4	Feral field	2012/2013	C	<0°C	Linear	231.89	-0.949	0.238	0.034
4	Scotland	2001	C	<0°C	Exponential	412.46	-0.011	0.983	<.0001
4	Oregon	2001	C	<0°C	Exponential	479.43	-0.044	0.860	0.005
4	Netherlands	2001	C	<0°C	Exponential	359.8	-0.006	0.892	<.0001
4	BC field	2012/2013	C	<0°C	Exponential	205.75	-0.002	0.033	<.0001
4	MA field	2012/2013	C	<0°C	Exponential	231.5	-0.002	0.057	<.0001
4	Feral field	2012/2013	C	<0°C	Exponential	255.16	-0.006	0.234	<.0001
5	Feral Field	2012/2013	F	<40°F	Exponential	414.08	-0.008	0.315	<.0001
5	Feral field	2012/2013	F	<40°F	Linear	355.54	-1.755	0.352	0.007

^a Linear equation: $GDD = A + B(F)$ where F is number of "frost days," A is the intercept, and B is the slope.

^b Exponential equation: $GDD = Ce^{D(F)}$ OR $\ln(GDD) = \ln(C) + D(F)$ where C is the intercept and D is the exponent.

temperatures are often quite warm before the onset of winter conditions and might otherwise accumulate a third or more of their total GDD before 1 January (Table 3).

Another possible explanation for the early hatch of feral eggs is that the bark on which they rest might absorb more solar heat than the paper tape in the mesh bags. However, the effect was as pronounced on the north-facing eggs, as it was for the south-facing ones, which suggests that differential solar heat gain is not

the explanation. It is possible that the difference arose from the laboratory rearing of the BC and MA eggs. More likely, microclimate differences between the bark surface and the mesh bags may account for the difference in accumulated temperature. Bakken (1989) describes substantial temperature differences between objects placed on or within 1 cm of tree boles due to thermal boundary layer effects on the bole surface.

Effects of Winter or Spring Cooling on GDD. As the number of frost days (daily minimum temperature

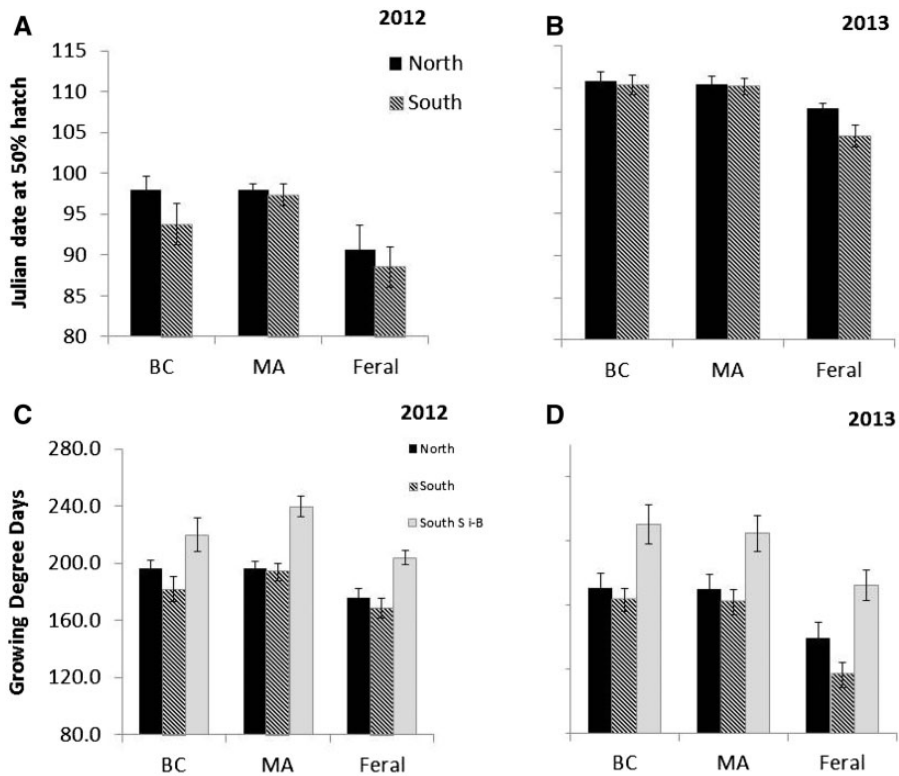


Fig. 3. Mean (\pm SE) number of Julian days to hatch in 2012 and 2013 (1 January start) for eggs held in mesh bags on the north and south sides of trees from females reared in laboratory from MA and BC compared with feral eggs laid by naturally occurring females on the same trees in MA in (A) 2012 and (B) 2013. The same data in (C) 2012 and (D) 2013 converted to mean GDD (\pm SE) to hatch per year (1 January start) for three egg groups on the north estimated from north-facing iButtons and eggs on the south with north-facing and south-facing iButton data.

Table 3. Date of hatch and GDD estimated for eggs oviposited and deployed on three different dates

Deployment date/egg group	Date at 50% hatch	GDD (Celsius)	
		Deployment date start	1 Jan. start
19 Nov. 2012	25 April 2013	299.46	208.52
4 Dec. 2012	24 April 2013	252.99	201.09
17 Dec. 2012	25 April 2013	225.38	208.52

was $< 0^{\circ}\text{C}$) increased, the number of GDD required for 50% hatch decreased (Fig. 4), and this was true for all egg groups in both years. Winter conditions lasted longer in 2013 compared with 2012, so the GDD accumulated by all three egg groups was less (Fig. 3). Our data from field sites for all three egg types were plotted on the same graph (Fig. 4) as that presented by Visser and Holleman (2001) with data from Oregon, Scotland, and the Netherlands. The MA field sites had more frost days than all three of those studies, but the MA field data fall out close to the same regression lines as those from Scotland and the Netherlands. It was expected that BC eggs would have similar GDD versus frost day regressions (Fig. 4) to those from Oregon (Kimberling

and Miller 1988, Visser and Holleman 2001), as southern Vancouver Island in BC, where we collected the winter moth larvae from which we obtained eggs, like Oregon, has relatively few frost days in winter. Instead, both BC and MA eggs were more similar to those from Europe (Fig. 4). Perhaps this pattern reflects an origin of winter moth in British Columbia and Massachusetts from a common source in Nova Scotia, where winter moth was first introduced to North America in the 1930s (Embree 1965). The Oregon moths may have been introduced separately from a different source (Kimberling and Miller 1988). The origin of different haplotypes of winter moth in North America was investigated, but not resolved, by Gwiazdowski et al. (2013).

Our data for feral eggs are also presented in Fahrenheit (Fig. 5), showing the difference between north-facing and south-facing eggs and the fact that linear and exponential models fit equally well (Table 2). Users who tabulated the number of frost days could use these regression equations to improve their ability to predict winter moth hatch rather than assuming a simple constant GDD that would apply across all years.

Winter moth eggs in 2012 and 2013 had accumulated very different GDD, when they hatched, presumably due to differences in frost days, as expected from the previous studies summarized by Visser and

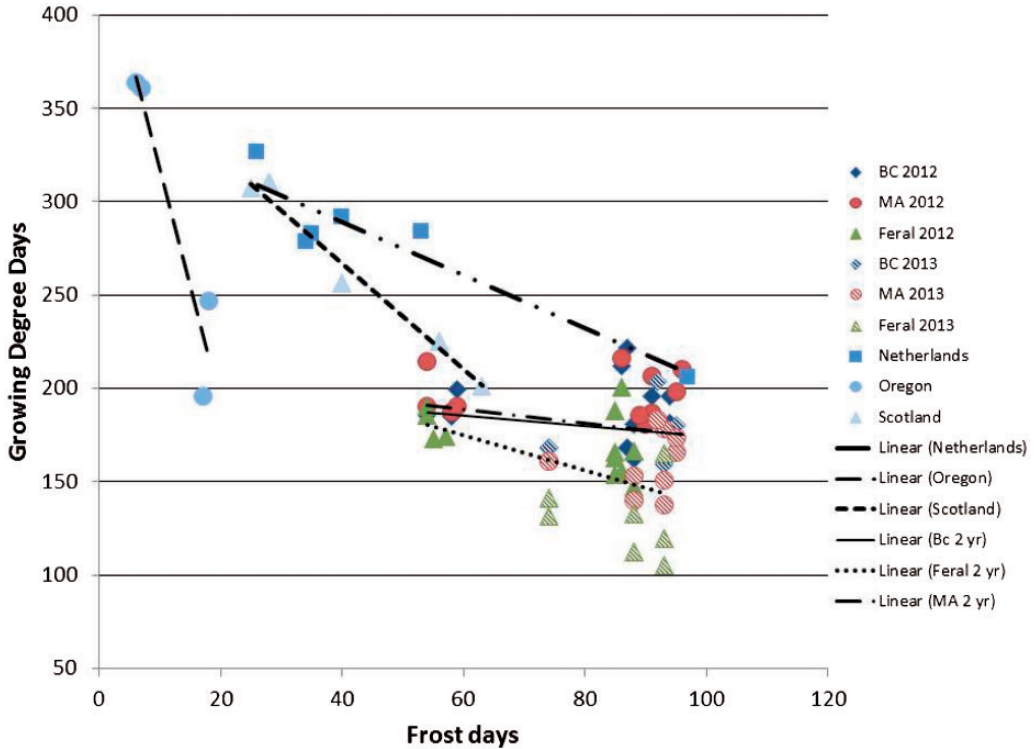


Fig. 4. Linear regressions of field eggs of bihourly GDD (Celsius) counted from 1 January to date of 50% hatch plotted versus number of frost days (days with temperatures $<0^{\circ}\text{C}$) counted from 1 December to date of 50% hatch and recorded with north-facing iButtons data compared with data presented by Visser and Holleman (2001) from studies conducted in Oregon, Scotland, and the Netherlands.

Holleman (2001). We cannot rule out, however, the possibility that other unknown differences between these two years might account for some or all of the differences in GDD.

Comparison of On-site GDD Estimates With Those From Online Sources. In Table 4, GDD estimates for north- and south-facing feral eggs made with north-facing iButtons were compared with the GDD estimates obtained online from www.uspest.org (Coop 2010) and NEWA (NEWA.cornell.edu 2014). GDD estimates made with 1 January, 1 February, and 1 March start dates were also compared. As explained above, we estimated GDD from our iButtons using bihourly accumulations of degree days (equation 2) and with GDD calculations based on the average of daily maximum and minimum temperatures (equation 3). The bihourly estimates of GDD with a 1 January start date were about 15% greater than the average Max-Min calculations of GDD. Similarly, the GDD estimates obtained from uspest.org implementing the sine wave correction (Baskerville and Emin 1969) produced estimates that were notably higher than those estimated from NEWA or from the iButton estimates of GDD from average of minimum and maximum temperatures (Table 4). The reason is that estimates of GDD based on daily average of maximum and minimum temperatures will seriously underestimate the degree day accumulation that nearly always occurs at midday, when the

average temperature ($(T_{max} - T_{min})/2$) is close to or below threshold. This fact has been known for many decades, and mathematical corrections have been proposed (e.g., Baskerville and Emin 1969), but these often have not been implemented on online Web sites, such as NEWA that estimate GDD. This error is illustrated with temperature data taken over one day (19 January 2013) at one field site (Fig. 6). This difference is reduced, however, if a 1 March start day is used. After 1 March, there are few days when the average temperature is close to or below threshold.

In Table 4, the mean deviation in GDD or days as a measure of goodness of fit was calculated for each of the field GDD estimates. The minimum value across all the different models is nearly always with the 1 March start date (Table 4). There were, however, no significant differences in deviations (paired comparisons of the 1 January and 1 March values at each iButton or weather station, $P > 0.05$) between the 1 January and 1 March start days for any of the different GDD estimates, so perhaps it matters little which start day is used.

Because date of oviposition in November and December had no effect on date of hatch, that implies that no GDD accumulated during these months. The severity of the winter, as indicated by the depth of minimum temperatures below freezing, also has no effect, as indicated by laboratory studies by Wylie (1960). The

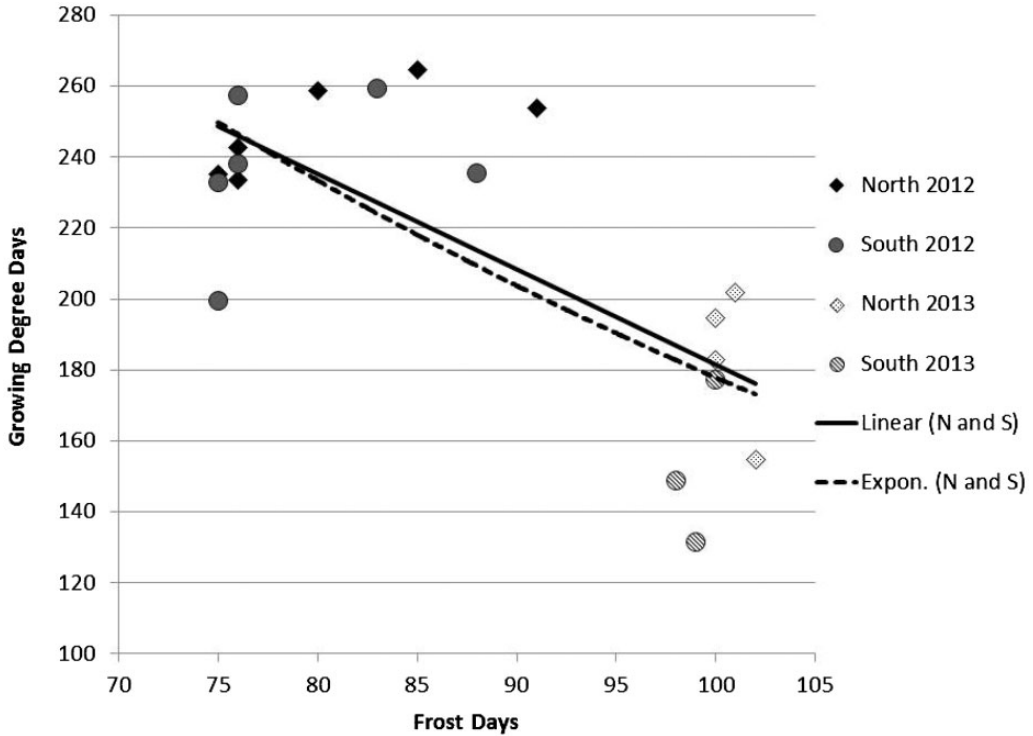


Fig. 5. Linear and exponential regressions of mean max/min GDD (Fahrenheit) for feral eggs counted from 1 January to date of 50% hatch plotted versus frost days (days with temperatures <0°C) counted from 1 December to date of 50% hatch recorded with north-facing iButtons.

Table 4. Mean growing degree day calculations (\pm SE) in Fahrenheit above a 40°F threshold temperature estimated from our on-site temperature recorders (iButtons) placed on the north side of trees and from Web site estimates of GDD from local weather stations (NEWA.cornell.edu and uspest.org) for feral eggs on the northern and southern side of trees each site for three GDD start dates over two years

	Start date	Bihourly GDD			uspest.org			MAX MIN GDD			NEWA GDD	
		1-Jan.	1-Feb.	1-Mar.	1-Jan.	1-Feb.	1-Mar.	1-Jan.	1-Feb.	1-Mar.	1-Jan.	1-Mar.
2012N iButton	Mean	268	232	182	319	279	227	243	223	204	239	197
	SE	6.67	5.20	182.25	6.21	7.72	7.76	5.20	3.96	3.81	5.47	7.23
	GDD deviation	23.84	24.09	4.89	34.96	38.93	28.37	27.40	28.92	23.41	25.85	24.79
	Day deviation	2.51	2.53	1.30	3.68	4.09	2.98	2.88	3.04	2.46	2.72	2.61
2013N iButton	Mean	219	177	168	230	182	167	177	150	147	177	136
	SE	12.63	11.45	11.68	6.00	6.33	6.32	7.31	7.69	8.64	5.40	6.01
	GDD deviation	38.86	41.81	24.78	56.18	61.00	38.18	41.56	46.19	35.98	39.40	38.40
	Day deviation	4.50	4.84	2.87	6.50	7.06	4.42	4.81	5.35	4.16	4.56	4.44
2 year N iButton	Mean	250	212	177	286	243	205	219	196	183	216	175
	SE	12.86	12.83	7.71	17.16	18.90	13.65	13.19	14.68	12.66	12.97	13.54
	GDD deviation	29.37	30.62	16.97	42.78	47.06	31.99	32.62	35.28	28.05	30.84	29.81
	Day deviation	3.09	3.22	1.78	4.50	4.95	3.36	3.43	3.71	2.95	3.24	3.13

Here, we compare the bihourly estimates of GDD °F versus average Max-Min estimates of the GDD °F from our iButtons and the average Max-Min estimates used by the online weather station estimates from NEWA.cornell.edu and uspest.org.

greater or lesser number of frost days in the northeastern United States is determined largely by weather conditions in March or April, as nearly every day in January and February of any year is a frost day. In other words, the frost day effect is a measure of whether the spring is early or late. In 2012, when the spring was early, the mean GDD with a January 1 start date in Fahrenheit above a 40°F threshold from uspest.org was 319 GDD \pm 6.21 SE (Table 4; range:

273–350 GDD). In 2013, when the spring was late, the same GDD values were 230 \pm 6.00 SE (Table 4; range 212–254 GDD). These values illustrate how much the varying number of frost days can change the estimated GDD. Users who record the number of frost days can use the regression equations given in Table 2 to make more accurate predictions. Users of the NEWA site to estimate GDD should note the much lower values of GDD given by that site (Table 4).

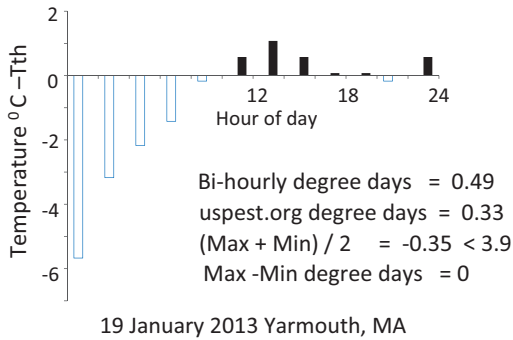


Fig. 6. Bihourly temperature record from 19 January 2013 at Yarmouth, MA, showing temperatures above a 3.9°F base accumulating degree days after 12 noon, whereas average temperature $((T_{max} + T_{min})/2)$ was below 3.9°F and therefore no Max–Min degree days accumulated that day.

In conclusion, our results are fundamentally consistent with those of previous investigators, who showed that GDD required for winter moth larval eclosion declined as the eggs were subjected to increasing days below freezing (Visser and Holleman 2001). In contrast to these reports, we found no difference in growing degree day requirements for winter moths collected from two regions with very different winter climates (Victoria, British Columbia, and eastern Massachusetts). Other sources of variation include the difference in dates of hatch between north-facing versus south-facing eggs, presumably due to solar heating. There remains, however, much unexplained variation in GDD requirements for winter moth hatch between sites within a year. Further work focusing on the physiological basis of factors that impede or promote larval eclosion is needed to help explain this variation.

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