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**EFFECT OF SPRING AND WINTER TEMPERATURES ON WINTER MOTH (GEOMETRIDAE:  
LEPIDOPTERA) LARVAL ECLOSION IN NEW ENGLAND**

A Thesis Presented

by

Emily L. Hibbard

Submitted to the Graduate School of the  
University of Massachusetts Amherst in partial fulfillment  
of the requirements for the degree of

MASTER OF SCIENCE

September 2014

Entomology

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**EFFECT OF SPRING AND WINTER TEMPERATURES ON WINTER MOTH (GEOMETRIDAE:  
LEPIDOPTERA) LARVAL ECLOSION IN NEW ENGLAND**

A Thesis Presented

by

EMILY L. HIBBARD

Approved as to style and content by:

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Department of Environmental Conservation

## **DEDICATION**

To Joe Elkinton and all of my coworkers at the USDA APHIS PPQ lab for their continued support and encouragement

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## ABSTRACT

### EFFECT OF SPRING AND WINTER TEMPERATURES ON WINTER MOTH (GEOMETRIDAE: LEPIDOPTERA) LARVAL ECLOSION IN NEW ENGLAND

SEPTEMBER 2014

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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. Growing degree days calculated from bi-hourly 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 based on bihourly temperature measurements, a 1 Jan start date and a 3.9°C developmental threshold was  $176.53 \pm 6.35SE$ .

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**CHAPTER 1**

**EFFECT OF SPRING AND WINTER TEMPERATURES ON WINTER MOTH LARVAL ECLOSION IN**

**NEW ENGLAND**

**1.1 Introduction**

Growing degree days (GDD) are widely used in agriculture 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 growing degree days assumes that rate of development, given by the inverse of the number of days to complete development, is a linear function of temperature. In fact, this function is almost never linear and various nonlinear models have been proposed (Logan et al. 1976). However, in the mid-range 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 Guy 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 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* (Roland and Embree 1995), and efforts are underway to introduce this fly into New England. To ensure success of the biocontrol agent, the parasitic flies must be allowed to emerge and subsequently 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 (Varley and Gradwell 1968, Roland and Embree 1995, Jepsen et al. 2008).

Timing of winter moth larval eclosion has been studied in Nova Scotia (Embree 1970), Oregon (Kimberling and Miller 1988), Scotland (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 292(°F) from a start date of 1 April, which in Nova Scotia was about six weeks before the winter moth larvae eclosed.

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 two months in southern Italy, but nearly eight months 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 intrinsic factors affect the duration of the egg stage. This study 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 Dec 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.

This 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 New England 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, Varley and Gradwell 1968, Jepsen et al. 2008).

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 to two on-line GDD calculators.

## **1.2 Materials and Methods**

### **1.2.1 Source of eggs.**

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 a 16°C growth chamber from June to November. In November, the temperature in both chambers was dropped to 10°C, and dropped again to 7°C ten days later to induce adult emergence. Adults were mated in groups of about ten males and ten females in small mesh bags. After the eggs were laid they were loosely shaken off the bags and stored at 7°C for no longer than 10 days until used in the experiments described below.

### **1.2.2 Laboratory studies.**

Eggs used in this study were laid within a six day 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 days. The photoperiod in this chamber was set to 8L:16D to simulate winter photoperiod. After that, dishes with eggs were moved to other growth chambers for rearing at

5°C, 10°C, 15°C, 20°C, or 25°C with a 16L:8D photoperiod. 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°C, 10°C, 15°C, 20°C, 25°C and data was 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:

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

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.

### 1.2.3 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 cm 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 bi-hourly 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 on three different dates. Egg groups were deployed on 19 November 2012, 4 December 2012, and 17 Dec. 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.

#### 1.2.4 Estimating Growing Degree Days.

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 to 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 bi-hourly temperature recordings from iButtons made over the period between egg deployment and hatch, as well as GDD estimates obtained from online sources.

Bi-hourly temperature data was used from field-deployed iButtons to calculate day degrees 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 day degrees from a specific start date (1 January, 1 February, or 1 March) up to the date of 50% hatch (Curry Guy 1987)(eq. 3.1).

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

for all  $T_{th} < (T_{ij}) < Max.T$ . Here  $T_{th} = 3.9^{\circ}C$  (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  $MaxT = 25^{\circ}C$ , which was the maximum temperature at which egg development was observed in the laboratory. For bi-hourly temperatures for which  $T_{ij} \leq T_{th}$ , no bi-hourly fractional degrees 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,

bi-hourly 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  $^{\circ}\text{C}$ ) \* 9/5. Here we use,  $T_{th}=40^{\circ}\text{F}$  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 website uspest.org.

### 1.2.5 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). 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 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 growing degree days from daily maximum and minimum temperatures:

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

whenever  $T_{th} < (T_{i,max} - T_{i,min})/2 < \text{max}T$ . Here  $T_{th}$  is the lower developmental threshold (in our case =  $40^{\circ}\text{F}$  or  $3.9^{\circ}\text{C}$ , 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  $\text{max}T$  is the upper developmental threshold ( $25^{\circ}\text{C}$  or  $70^{\circ}\text{F}$ ) 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  $((T_{i,max} - T_{i,min})/2) > \text{max}T$  the day degrees accumulated on that day is  $\text{max}T - T_{th}$ . 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 from degree days was converted to days by dividing average GDD deviation by the mean number of day degrees 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.

### **1.2.6 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 growing degree days 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 Dec 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 for GDD in Fahrenheit for our data from feral eggs were made.

### **1.2.7 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 HSD 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 Massachusetts (MA) or British Columbia (BC).

### **1.3 Results and Discussion**

#### **1.3.1 Laboratory Results**

##### **1.3.1.1 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°C, 10°C, 15°C and 20°C for each of the groups held for different numbers of days at 1°C. We dropped the data for 5°C and 25°C for these regressions because at these temperature extremes, the inherent nonlinearity of the rate of development plotted versus temperature (Logan et al 1976) are evident and would thus distort the linear regression estimates of GDD, which always work best at the mid-range of temperatures. The plots for the eggs from Massachusetts (MA) were very similar to those for the eggs from British Columbia (BC). The regression lines shown 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  $3.55^{\circ}\text{C} \pm 0.30\text{SE}$  for BC eggs and  $3.67^{\circ}\text{C} \pm 0.31\text{SE}$  for MA eggs (Table 1). These estimates are quite close to the 3.9°C threshold estimated by those of 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 42 days 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.

### **1.3.2 Field Results.**

#### **1.3.2.1 North vs. South-facing Eggs.**

Eggs from all three sources hatched about three weeks earlier in 2012 than in 2013 (Fig. 3 A, B). South-facing eggs hatched on average 1.6 days earlier than north-facing eggs in both years (paired t-test,  $t = 2.99$ ,  $df = 27$ ,  $P = 0.006$ ). By converting the data to GDD (Fig. 3 C, D) most, but not all, of the differences between years was accounted for. We assumed 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 on the north and south side would be nearly equal. Such was not the case. South-facing iButtons recorded far more GDD when the eggs hatched on that side of the tree compared to the north-facing iButtons (Fig. 3 C, D; paired t-test,  $t = -3.44$ ,  $df = 28$ ,  $P = 0.002$ ). 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 or made out of metal, they absorbed more heat. 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 data are comparable to those collected by most other researchers and users, who will collect data from weather stations with shaded temperature sensors. These include the weather stations generating data for the online GDD estimates.

#### **1.3.2.2 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; ANOVA,  $F = 7.17$ ,  $df = 2,29$   $P = 0.003$ ) and in GDD (Fig. 3C,D; ANOVA,  $F = 6.52$ ,  $df = 2,30$   $P = 0.004$ ) There were, however, no significant differences in hatch dates (Fig. 3 A, B, or GDD (Fig. 3 C,D, Tukey's HSD,  $\alpha = 0.05$ ) 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 in 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. 3 A, B ;Tukey's HSD,  $\alpha = 0.05$ ). 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 two weeks 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 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 (see Table 3).

Another explanation for the early hatch of feral eggs might be 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 difference arose from the laboratory rearing of the BC and MA eggs. More likely, some unknown microclimate difference between the bark and the mesh bags may account for the difference.

### **1.3.2.3 Effects of winter or spring cooling on GDD**

As the number of frost days (daily minimum temperature 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 to 2012, so the GDD accumulated by all three egg groups was less (Fig. 4), which is why GDD was less. Our data from field sites for all three egg types was plotted on the same graph (Fig. 4) as that presented by Visser and Holleman 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 vs. frost day regressions (Fig 4) to those from Oregon (Kimberling and Miller 1988, Visser and Holleman 2001), since southern Vancouver Island in British Columbia (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. The origin of different haplotypes of winter moth in North America was investigated, but not resolved, by Gwiazdowski (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 compared with 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 Holleman (2001). However, we cannot rule out the possibility that other unknown differences between these two years might account for some or all of the differences in GDD.

#### **1.3.2.4 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 uspest.org (Coop 2010) and NEWA (NEWA.cornell.edu 2014). GDD estimates made with 1 Jan, 1 Feb and 1 March start dates were also compared. As explained above, we estimated GDD from our iButtons using bi-hourly accumulations of degree days (eq. 2) and with GDD calculations based on the average of daily maximum and minimum temperatures (eq. 3). The bi-hourly estimates of GDD with a 1 Jan 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 average temperatures (Table 4). The reason is that estimates of GDD based on daily average of maximum and minimum temperatures will seriously underestimate the day-degree accumulation that nearly always occurs at midday when the average temperature  $(\text{Min} + \text{Max}) / 2$  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 the online websites, 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 1 March start date. There was, however, no significant difference in deviations between the 1 Jan and 1 March start days for any of the weather station data, so perhaps it matters little which start day is used.

Since 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 greater or lesser number of frost days in New England is determined largely by weather conditions in March or April, since 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  $319 \text{ GDD} \pm 6.21\text{SE}$  (Table 4; range: 273-350 GDD). In 2013, when the spring was late, the same GDD values were  $230 \pm 6.00\text{SE}$  (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).

#### **1.4 Conclusion**

Our results are fundamentally consistent with those of previous investigators who showed that growing degree days 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 vs. 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.

**Table 1.** Laboratory estimates of developmental threshold temperature and number of growing degree days required for hatch of eggs held at 1° C for different numbers of days. Estimates are generated from linear regressions shown in Fig. 1. Eggs were oviposited by female winter moths collected as larvae from sites in Massachusetts (MA) or Vancouver Island in British Columbia (BC) and then reared to the adult stage in growth chambers.

# days in chill	<u>developmental threshold temp Celsius</u>		<u># Growing Degree Days Celsius</u>	
	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
<b>Mean</b>	3.67	3.55		
<b>SE</b>	0.31	0.30		

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

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



**Table 2.** Linear and exponential regression coefficients of growing degree days as a function of days in chill in the laboratory (Fig. 2) or days with temperatures  $< 0^{\circ}\text{C}$  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	$^{\circ}\text{C}$ or $^{\circ}\text{F}$	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	$<0^{\circ}\text{C}$	Linear	381.19	-2.856	0.977	0.002
4	Oregon	2001	C	$<0^{\circ}\text{C}$	Linear	442.2	-12.516	0.902	0.050
4	Netherlands	2001	C	$<0^{\circ}\text{C}$	Linear	345.57	-1.417	0.866	0.007
4	BC field	2012/2013	C	$<0^{\circ}\text{C}$	Linear	202.88	-0.288	0.029	0.451
4	MA field	2012/2013	C	$<0^{\circ}\text{C}$	Linear	211.11	-0.374	0.057	0.285
4	Feral field	2012/2013	C	$<0^{\circ}\text{C}$	Linear	231.89	-0.949	0.238	0.034
4	Scotland	2001	C	$<0^{\circ}\text{C}$	Exponential	412.46	-0.011	0.983	<.0001
4	Oregon	2001	C	$<0^{\circ}\text{C}$	Exponential	479.43	-0.044	0.860	0.005
4	Netherlands	2001	C	$<0^{\circ}\text{C}$	Exponential	359.8	-0.006	0.892	<.0001
4	BC field	2012/2013	C	$<0^{\circ}\text{C}$	Exponential	205.75	-0.002	0.033	<.0001
4	MA field	2012/2013	C	$<0^{\circ}\text{C}$	Exponential	231.5	-0.002	0.057	<.0001
4	Feral field	2012/2013	C	$<0^{\circ}\text{C}$	Exponential	255.16	-0.006	0.234	<.0001
5	Feral Field	2012/2013	F	$<40^{\circ}\text{F}$	Exponential	414.08	-0.008	0.315	<.0001
5	Feral field	2012/2013	F	$<40^{\circ}\text{F}$	Linear	355.54	-1.755	0.352	0.007

**Table 3.** Date of hatch and growing degree days estimated for eggs oviposited and deployed on three different dates

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<u>deployment date/egg group</u>	<u>date at 50% hatch</u>	<u>deployment date start</u>	<u>GDD (Celsius)</u> <u>1 Jan start</u>
Nov. 19, 2012	4/25/2013	299.46	208.52
Dec. 4, 2012	4/24/2013	252.99	201.09
Dec. 17, 2012	4/25/2013	225.38	208.52

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**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 website 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. Here we compare the bi-hourly 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.

start date	bi-hourly GDD			uspest.org GDD			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	
<b>2012</b>	MEAN	268	232	182	319	279	227	243	223	204	239	197
	Std. Error	6.67	5.20	182.25	6.21	7.72	7.76	5.20	3.96	3.81	5.47	7.23
<b>N iButton</b>	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
<b>2013</b>	MEAN	219	177	168	230	182	167	177	150	147	177	136
	Std. Error	12.63	11.45	11.68	6.00	6.33	6.32	7.31	7.69	8.64	5.40	6.01
<b>N iButton</b>	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
<b>2 year</b>	MEAN	250	212	177	286	243	205	219	196	183	216	175
	Std. Error	12.86	12.83	7.71	17.16	18.90	13.65	13.19	14.68	12.66	12.97	13.54
<b>N iButton</b>	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

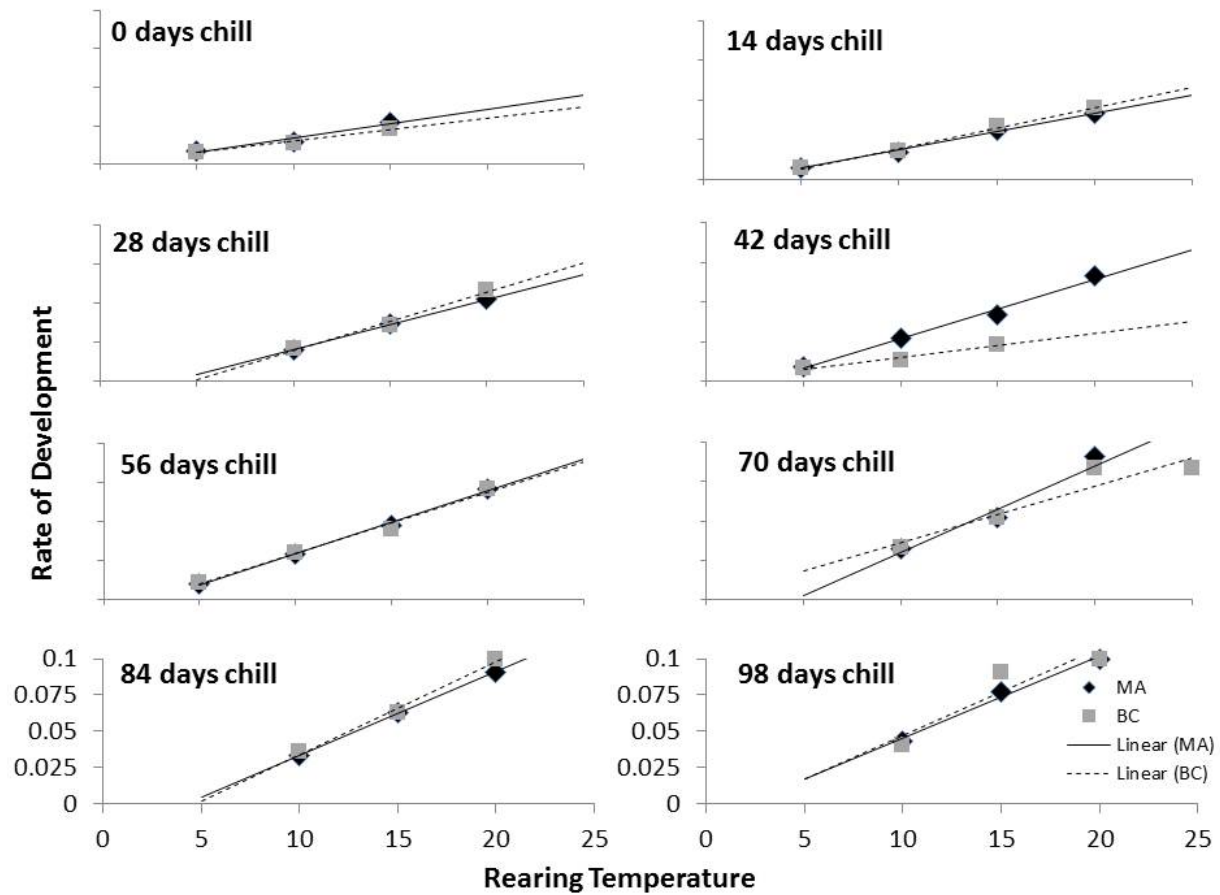


Figure 1. Linear regressions of rate of development ( $1/(\text{number of days to } 50\% \text{ hatch})$ ) plotted versus rearing temperature in laboratory growth chambers for winter moth eggs laid by females reared from larvae collected from Massachusetts (MA) or British Columbia (BC) and held for different numbers of days in chill ( $1^{\circ}\text{C}$ ) after oviposition before rearing at higher temperatures. We used these regressions to determine the developmental threshold and growing degree days for each chill group (see Table 1)

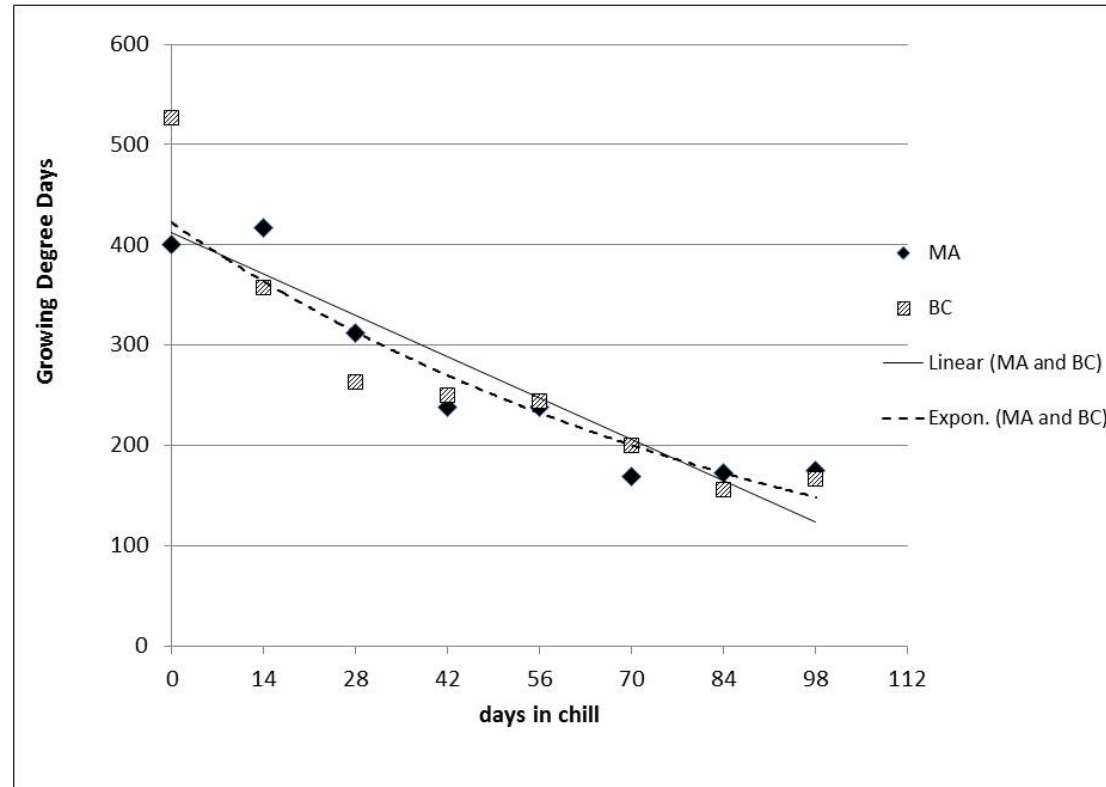


Figure 2. Linear and exponential regressions of the growing degree days (GDD) estimated as in Table I plotted versus number of days in chill for eggs from moths from Massachusetts (MA) and British Columbia (BC) shown in Fig 1.

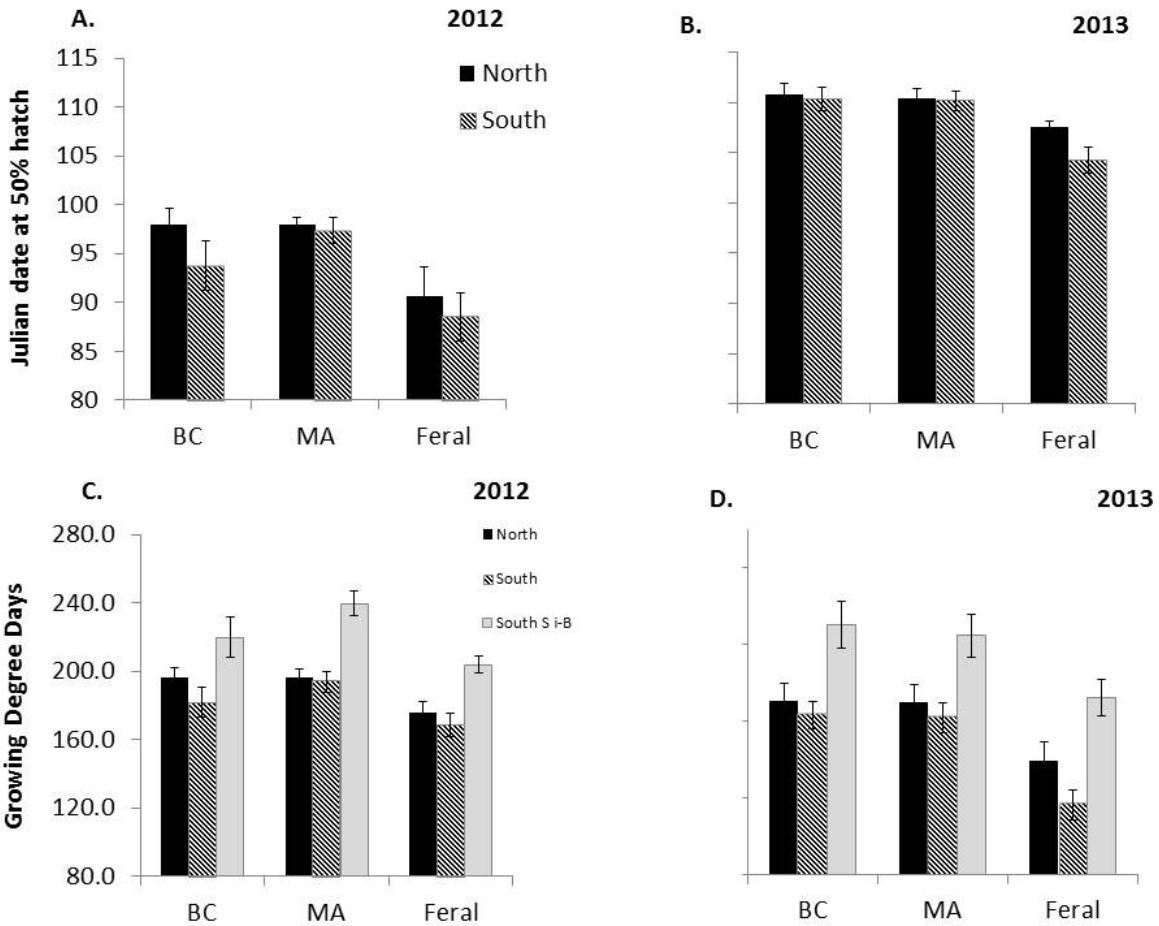


Figure 3. Mean ( $\pm$ SE) number of Julian days to hatch in 2012 and 2013 (1 Jan start) for eggs held in mesh bags on the north and south sides of trees from females reared in laboratory from Massachusetts (MA) and British Columbia (BC) compared to feral eggs laid by naturally occurring females on the same trees in Massachusetts in A) 2012 and B) 2013. The same data in C) 2012 and D) 2013 converted to mean GDD ( $\pm$ SE) to hatch each year (in  $^{\circ}$ C above 3.9 $^{\circ}$ C threshold, 1 Jan start) for three egg groups on the north estimated from north-facing I-Buttons and eggs on the south with north side and south side iButton data.

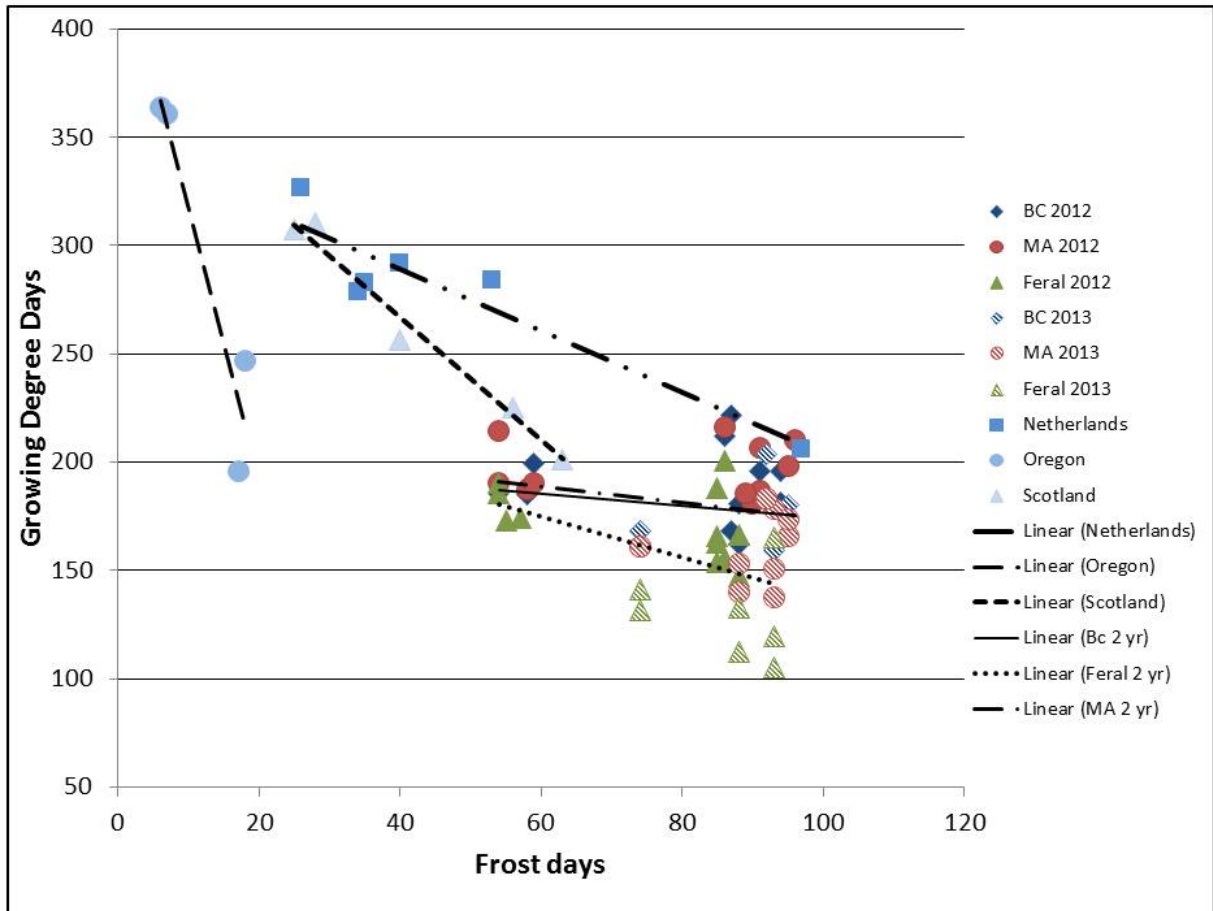


Figure 4. Linear regressions of field eggs of bi-hourly GDD (Celsius) counted from 1 January to date of 50% hatch plotted versus number of frost days <0°C counted from 1 Dec to date of 50% hatch ) and recorded with north-facing iButtons data compared to data presented by Visser and Holleman (2001) from studies conducted in Oregon, Scotland and the Netherlands

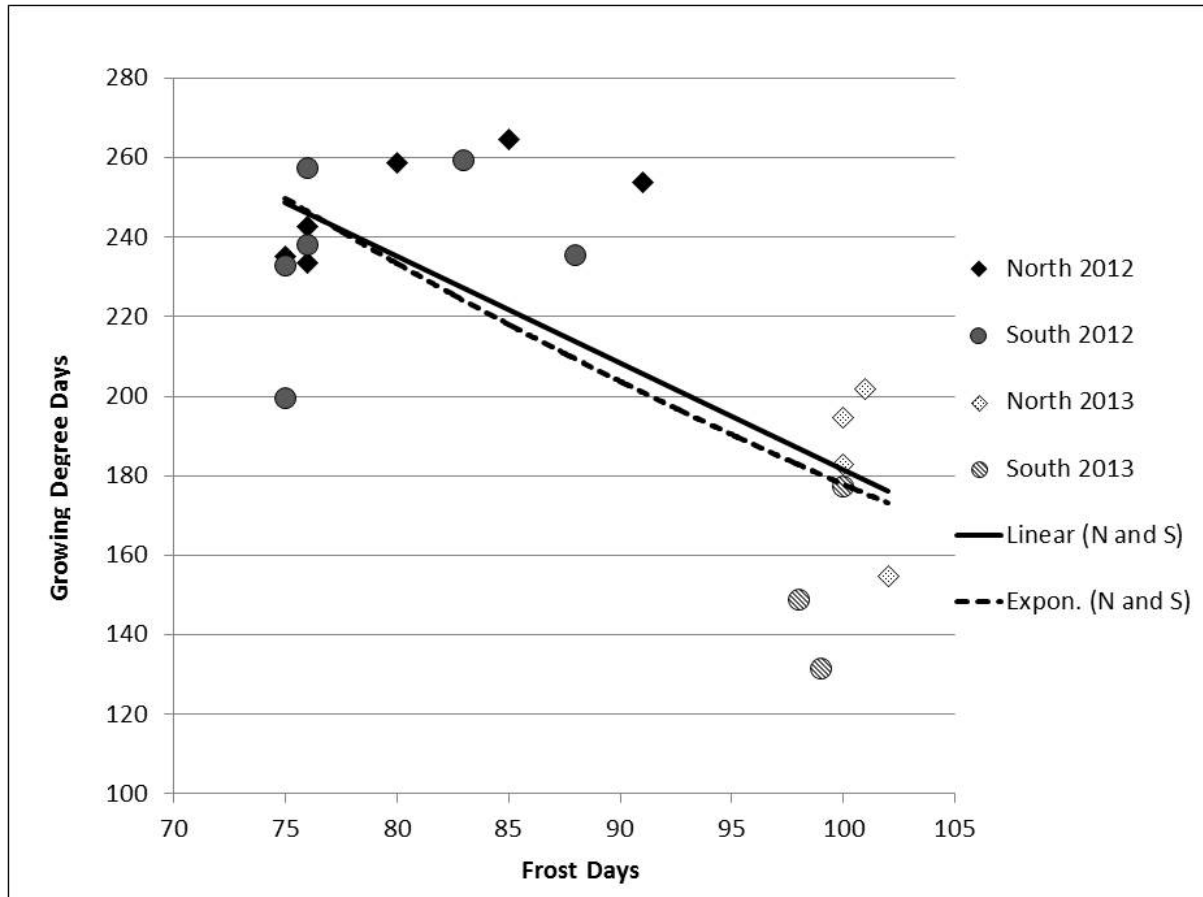
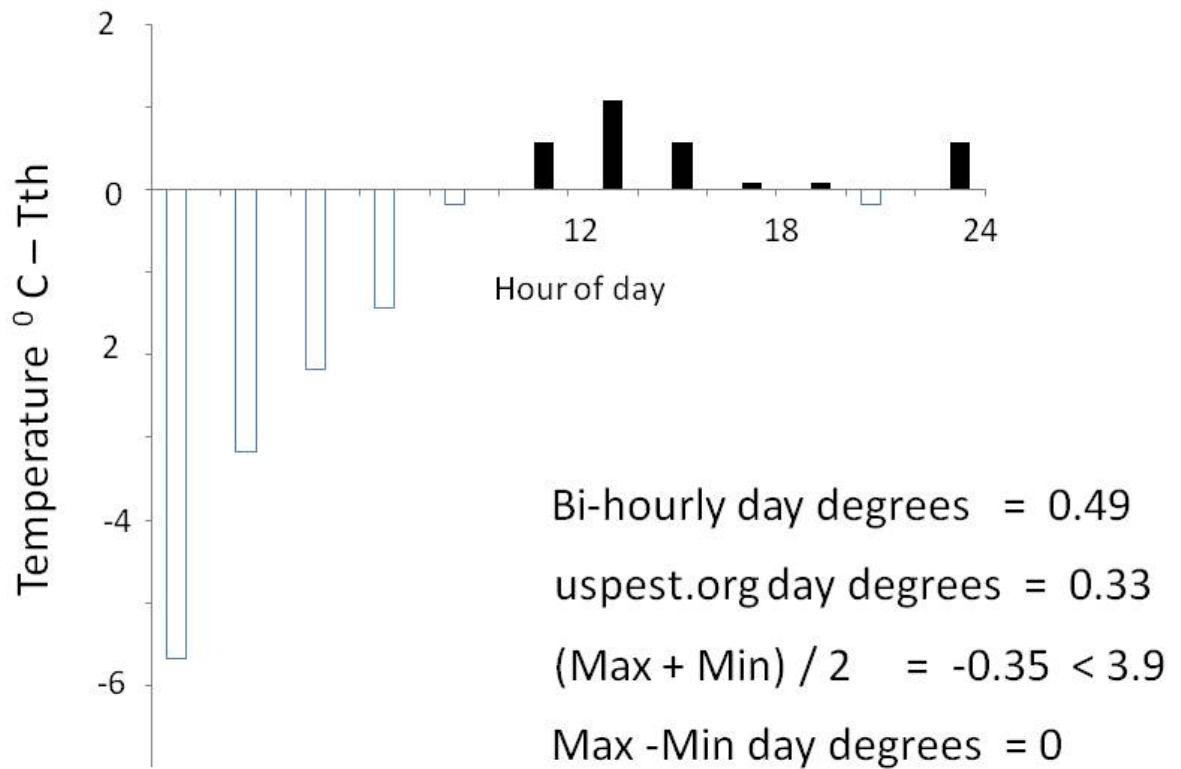


Figure 5. Linear and exponential regressions of bi-hourly mean max/min GDD (Fahrenheit) from the iButton data for feral eggs counted from 1 January to date of 50% hatch plotted versus frost days <math>0^{\circ}\text{C}</math> counted from 1 Dec to date of 50% hatch recorded with north-facing iButtons





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Figure 6. Bi-hourly temperature record from 19 January 2013 at Yarmouth MA showing temperatures above a 3.9°C base accumulating day degrees after 12 noon, whereas average temperature  $(T_{\text{max}} + T_{\text{min}})/2$  was below 3.9°C and therefore no max-min degree days accumulated that day

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