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Effects of Low Temperature and Delayed Mating on Pine Looper (*Bupalus piniarius*) Fecundity

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Unfavourable weather during an insect's oviposition period may result in reduced egg-laying opportunities. This, in turn, may lead to a reduction in realised fecundity. In nature, temperature conditions may deviate considerably from what is optimal for the insect, but unfavourable conditions seldom last for long time periods. Little is known about effects of periodic low temperatures on the ecology of insects. Effects of four-day periods of consistent low temperature (10 °C) and four days delayed mating on pine looper *Bupalus piniarius* fecundity were studied in laboratory experiments. Some females were exposed to low temperature directly after eclosion while others were exposed to low temperature two days after eclosion. Low temperature had a drastic effect on *B. piniarius* oviposition rate. Very few eggs were laid at this temperature. Females experiencing a short period of 10 °C had lower realised fecundity. However, overall differences were small, especially when females had experienced two days of normal temperature (20 °C) prior to the low temperature. There were no differences in number of eggs and amount of fat retained at death among treatments. Females that experienced low temperature had a higher oviposition rate after low temperature application and lived longer. Females that experienced delayed mating at normal temperature laid 30% of their eggs prior to mating, while females experiencing delayed mating combined with low temperature only laid 0.4% of their eggs before mating. Those unfertilised eggs were non-viable, thereby reducing realised fecundity.

Keywords: *Bupalus piniarius*, oviposition, realised fecundity, temperature, delayed mating

Introduction

Potential fecundity is often used to predict future insect population density. It is well known, however, that realised fecundity, the number of eggs actually laid, may differ substantially from potential fecundity (Leather 1988). There is a number of factors that influences realized fecundity in herbivorous insects, e.g. availability and quality of the host plant (Papaj 2000; Šmits *et al.* 2001), predation pressure (Tammaru et al. 1996), mating success (Vickers 1997), and temperature (Caroll & Quiring 1993).

Generally, there is an optimum temperature above and below which realized fecundity decreases (e.g. Carroll & Quiring 1993). In nature, temperature conditions may deviate considerably from what is optimal for the insect, but unfavourable conditions seldom last for long time periods. Even short periods of adverse weather conditions can significantly affect fecundity, for example, when temperature has a strong effect on adult behaviour (Greenfield & Karandinos 1976). Thus, it is ecologically more relevant to assess the effects of short periods of unfavourable temperature regimes (e.g. periodic low temperatures) than constant non-optimal temperatures.

In this paper the effects of relatively low temperature (10 °C) on pine looper moth *Bupalus piniarius* L. (Lepidoptera: Geometridae) oviposition rate are reported. Most *B. piniarius* eggs are laid during the first few days after eclosion (Botterweg 1978; Šmits *et al.* 2001), therefore, the effect of temperature-induced low oviposition rate on realised fecundity can be expected to be most severe if it occurs early in the adult lifetime. This hypothesis was tested in a laboratory setting by subjecting *B. piniarius* to low temperature for four days immediately after adult eclosion or kept at normal temperature (18-20 °C) for two days prior to exposure to low temperature.

Non-favourable weather conditions may affect insect fecundity directly by disrupting oviposition, but may be also associated with other factors, such as delayed mating. Effects of delayed mating vary among lepidopteran species. Some species can tolerate more than a week of delayed mating without significant effects on fecundity (e.g. Kehat & Gordon 1975). For some other lepidopteran species, however, delayed mating reduces reproductive capacity (e.g. Kiritani & Kanoh 1984; Leather *et al.* 1985).

In this study the interaction between the temperature and delayed mating was of particular interest. A hypothesis was posed that the effects of delayed mating are less pronounced at lower temperatures because adults have a longer life span and slower egg maturation rate. This hypothesis was tested in a laboratory experiment. The interaction between temperature and delayed mating on realized fecundity, adult longevity and egg fertility was also examined.

Materials and methods

Study organism

The pine looper moth, *Bupalus piniarius*, is a univoltine forest pest that occasionally defoliates its host tree Scots pine, *Pinus sylvestris* L. *B. piniarius* has a long history as a pest in Europe (e.g. Butovitsch 1946; Klimatzek 1972; Barbour 1985). In Sweden, the adult flight period starts in mid - late June. Moths copulate in the canopy and soon afterwards start laying eggs in rows on needles (one to 25 eggs per batch). Moths do not feed. Eggs hatch after 14-20 days, pass through four to seven instars and descend to the ground for pupation in October-November (Gruys 1970). *B. piniarius* overwinters as a pupa in the soil. More information on *B. piniarius* biology can be found in Barbour (1988).

Weather (e.g. precipitation and drought) is thought to be an important factor in the population dynamics of *B. piniarius* (Barbour 1988; Broekhuizen et al. 1993). Outbreaks are often preceded by periods of drought, although no definitive correlation to dry weather has been found (Barbour 1988).

Effect of temperature and delayed mating on realised fecundity

In order to investigate the effects of low temperature and delayed mating on *B. piniarius* fecundity, laboratory experiments were initiated in the summer of 1999. Pupae were collected from a field population in Latvia (57°30'N, 22°07'E), sorted by sex, and female pupae were segregated into 5 mg weight classes. Females were assigned to the different treatments so that all weight classes would be similarly represented. The first replicate was started on June 11and the last one on June 20. The number of replicates and the average pupal weights were: $n_{1,1}$ (normal temperature, normal mating) = 21, weight = 120±4 mg (fresh weight) ($\bar{X}\pm$ s.e.); $n_{1,2}$ (normal temperature, delayed mating) = 22, weight = 119±3 mg; $n_{2,1}$ (low temperature, normal mating) = 23, weight = 118±3 mg; $n_{2,2}$ (low temperature, delayed mating) =22, weight = 117±4 mg.

The experiment was conducted in constant environment rooms (L20:D4 h, r.h. 70%) at two temperatures. The temperature regimes used in the experiment were designated 20 °C (range 18-20 °C) during the entire adult life (normal), and four to five days low temperature designated 10 °C (range 6-10 °C) immediately after eclosion, followed by normal temperature for the rest of the adult life. Females were allowed to mate either immediately after eclosion (normal) or four days after eclosion (delayed). In the normal mating treatments adults were moved in pairs (male+female) to small cages and after females had been observed to mate they were moved to pine branches at one of the two temperatures for oviposition. The pine branches were individually placed in containers with water and enclosed in transparent plastic cylinders (height 25 cm, diameter 12.5 cm) with the top covered by muslin. Emerging females were supplied with water. In the delayed mating treatments virgin females were moved to the pine branches in one of the two environment rooms immediately after eclosion and remained unmated for four days (for females at low temperature this period coincided with the time they spent at low temperature). Branches were examined for eggs and replaced daily.

Longevity and daily oviposition rate were recorded for each female. After death females were dissected and the remaining fully developed eggs counted. The amount of fat left in females at death was evaluated and assigned to one of four arbitrary classes (0 to 3): 0 – no fat left, 3 – large amount of fat left.

Effect of timing of low temperature on pine looper fecundity

An experiment was conducted in 2000 to assess whether periods of low temperature occuring at different times after eclosion differentially affect realized fecundity. Pupae were collected from a field population in south Sweden (57°00'N, 15°20'E) and handled as described above. One factor (temperature) with three treatments was studied. Two treatments were the same as in 1999: normal temperature and low temperature during four days immediately after eclosion. In a third treatment, females were exposed to low temperature for four days after experiencing normal temperature for two days. The number of replicates and average pupal weights were: for normal temperature $n_{3,1}$ = 22, weight = 128±4 mg; low temperature $n_{3,2}$ = 22, weight = 131±2 mg; low temperature after two days $n_{3,3}$

= 27, weight = 128±4 mg. Realized fecundity, the number of eggs laid per day, and eggs and fat retained at death were estimated as in the 1999 experiment.

Data analyses

Analysis of covariance was used to analyse effects of temperature and delayed mating on realized fecundity, longevity and number of eggs retained at death. Female pupal weight was used as the covariate because fecundity correlates to weight (Figure 1). The Kruskal-Wallis test was used to assess the differences in fat resources left at death.

Results

During the initial four-day confinement at low temperature females had an extremely low oviposition rate (Fig. 2b, d; Fig. 3). Mean oviposition rate for females exposed to low temperature in 1999 was 0.98±0.34 ($\bar{X}$ ± s.e.) eggs per day and only seven females out of 47 laid any eggs at all. There were no eggs laid by females kept at low temperature in 2000.

The low oviposition rate at 10 °C decreased overall realised fecundity. In both years, females that had experienced low temperature for four days laid fewer eggs compared to females at constant normal temperature (significant temperature effect, Table 1 (1999) and Table 2, Figure 1 (2000)). In 1999, females at normal temperature laid 144±5 (grand mean, $\bar{X}$ ± s.e.) eggs, while females that experienced low temperature laid 114±6 eggs. Average fecundity in separate treatments from both years is summarized in Table 3.

There were no differences in the number of eggs laid between treatments with normal and delayed mating (Table 1). However, for females exposed to normal temperature and delayed mating a significant proportion of eggs (30.1%) was laid before mating, resulting

Table 1. General Linear Model procedure for test of the hypothesis that temperature and delayed mating affect *Bupalus piniarius* realised fecundity, number of fertile eggs laid, number of eggs retained at death, and adult longevity. Treatments are i) temperature: normal temperature (20 °C) and low temperature (females kept at 10 °C for 4-5 days after eclosion); ii) mating: normal mating (females mated just after eclosion) and delayed mating (females mated four days after eclosion). Pupal weights used as covariates.

Source	d.f.	Realised fecundity		Fertilised eggs laid		Eggs retained		Adult longevity	
		F	P>F	F	P>F	F	P>F	F	P>F
Temperature	1	15.38	0.0002	1.00	0.3193	3.83	0.0539	24.25	0.0001
Mating	1	0.17	0.6856	9.63	0.0026	0.00	0.9570	1.14	0.2895
Temperature*Mating	1	0.92	0.3392	12.75	0.0006	0.07	0.7917	18.82	0.0001
Weight (covariate)	1	18.29	0.0001	18.18	0.0001	1.19	0.2790	0.28	0.5953
Error	83								

Table 2. General Linear Model procedure for test of the hypothesis that temperature affects *Bupalus piniarius* realised fecundity, number of eggs retained at death, and adult longevity. Treatments are i) normal temperature (20 °C), ii) low temperature (10 °C) for four days after eclosion, iii) four days low temperature applied two days after eclosion. Pupal weights used as covariates

Source	d.f.	Realised fecundity		Eggs retained		Adult longevity	
		F	P>F	F	P>F	F	P>F
Temperature	2	4.14	0.0202	1.17	0.3175	14.04	0.0001
Weight (covariate)	1	91.35	0.0001	0.00	0.9663	1.90	0.1725
Error	67						
Contrast							
Normal vs low t° after 2 days	1	4.70	0.0337	2.33	0.1313	20.9	0.0001

Table 3. Mean realised fecundity ± s.e. of females from different treatments in 1999 and 2000 experiments. Normal temperature represents 20 °C, low temperature represents 10 °C. Mating was delayed for four days

Year	Normal temperature		Four days low temperature from the eclosion		Four days low temperature applied two days after eclosion
	Normal mating	Delayed mating	Normal mating	Delayed mating	Normal mating
1999	149.8±7.1	139.2±6.2	112.4±9.2	115.9±9.4	
2000	160.1±6.8	-	142.7±6.0	-	150.9±6.4

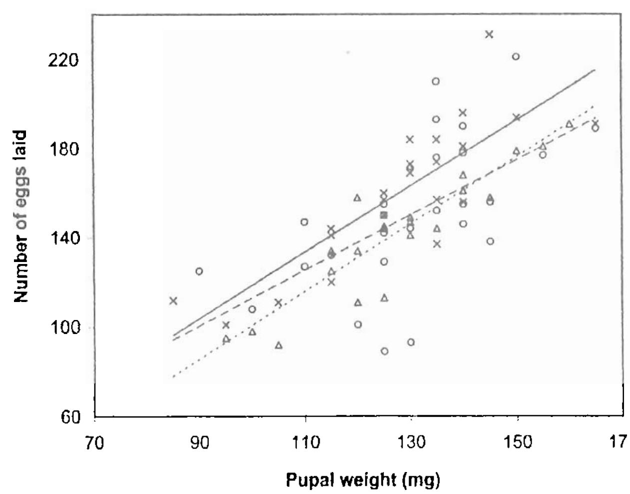

Figure 1. Effect of low temperature (10 °C) on *Bupalus piniarius* realised fecundity. Crosses and solid line represent females kept at 20 °C (control) (y= 1353.4x - 12.665, n = 22, R^2 = 0.552, P<0.001); circles and dashed line represent females experiencing low temperature (10 °C) for four days starting two days after eclosion and for the rest of the time kept at 20 °C (y = 1245.4x - 11.665, n = 27, R^2 = 0.3701, P<0.001); triangles and dotted line represent females experiencing low temperature (10 °C) for four days and thereafter kept at 20 °C (y = 1564.9x - 64.716, n = 22, R^2 = 0.4323, P<0.001)

in significantly fewer fertile eggs (mating effect, Table 1, Figure 2b). Females kept at low temperature only laid 0.4% of their eggs before mating. The difference in number of fertilized eggs laid at different temperatures is illustrated by a significant temperature by mating interaction (Table 1).

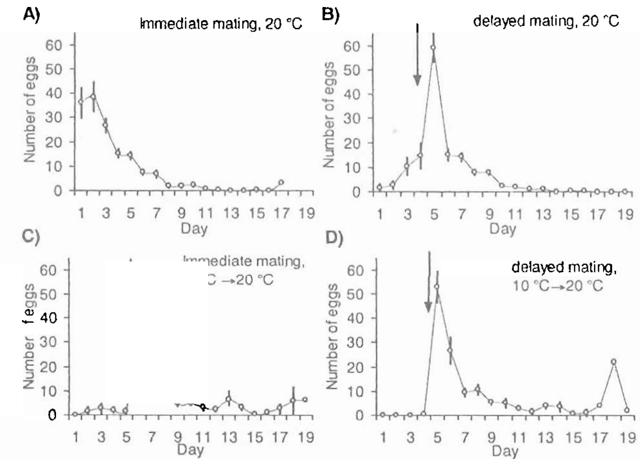

Figure 2. Daily oviposition rate ($X \pm$ s.e.) of *Bupalus piniarius* from a laboratory experiment in 1999: A) females mated immediately after eclosion and kept at 20 °C; B) females mated four days after eclosion and kept at 20 °C; C) females mated immediately after eclosion and experiencing low temperature (10 °C) for four to five days and further kept at 20 °C; D) females mated four days after eclosion and experiencing low temperature (10 °C) for four days and thereafter kept at 20 °C. Arrow denotes the end of the treatment: low temperature or delay in mating

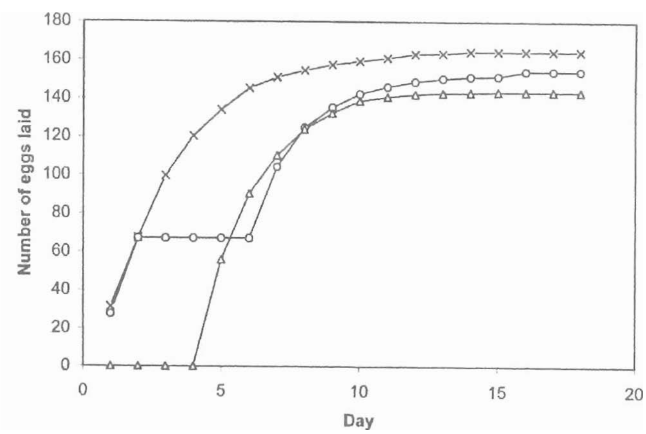

Fig. 3. Cumulative oviposition of mated *Bupalus piniarius* females from a laboratory experiment in 2000: crosses represent females kept at 20 °C; circles represent females experiencing low temperature (10 °C) for four days starting two days after eclosion and for the rest of the time kept at 20 °C; triangles represent females experiencing low temperature (10 °C) for four days and thereafter kept at 20 °C

The number of eggs retained did not differ among treatments in any of the years (Tables 1 and 2). On average, females retained 11.8±2.7 eggs ($X \pm$ s.e.) in 1999 and 4.3±0.8 eggs in 2000. Low temperature had a significant effect on longevity. Females that experienced low temperature for four days lived, on average, three days longer than females at normal temperature (Tables 1 and 2). Unmated females at high temperature lived three days longer than females with normal mating. The amount of fat at death did not differ among treatments (Kruskall-Wallis test, in 1999 $\chi^2 = 2.959$, df = 3, P = 0.40; in 2000 $\chi^2 = 0.634$, df = 2, P = 0.73).

Discussion

A decrease in temperature to 10 °C almost completely arrested *Bupalus piniarius* oviposition. Very few eggs were laid during exposure to low temperature. Few data of this kind have previously been reported. In one case, another lepidopteran species, *Synanthedon pictipes*, did not lay any eggs when temperature was decreased by ten degrees below optimum (Greenfield & Karandinos 1976). The strong temperature effect on *B. piniarius* oviposition rate cannot be explained by retarded egg maturation because adult females emerge with a large proportion of eggs already mature (Šmits et al. 2001), and oviposition begins soon after eclosion.

There was a difference in realised fecundity between females kept at a constant temperature of 20 °C and females that experienced one short period of 10 °C. The effect was smaller when females were exposed to the low temperature two days after eclosion because they laid a considerable proportion of their eggs beforehand. Even though the differences in realized fecundity were statistically significant, absolute differences were only 21% in 1999 and 11% in 2000. However, even such a decrease in realized fecundity illustrates the importance of weather factors for the failure of *B. piniarius* females to attain their potential fecundity.

Pine looper females under natural conditions usually attain less than 50% of their potential fecundity (cf. Klomp 1966; Broekhuizen et al. 1994; Marchenko 1994), which is a much larger reduction than that found in this study. Several factors could have contributed to a less than expected reduction in realised fecundity. First, a significantly higher oviposition rate was observed after the period of low temperature as compared to the corresponding period for females at normal temperature. This type of response has also been documented for the cotton leaf-worm, *Spodoptera littoralis* (Kehat & Gordon 1975). However, in other insects oviposition rate does not always increase after unfavourable conditions (Kiritani & Kanoh 1984; Carey et al. 1998). Second, *B. piniarius* females exposed to 10 °C lived significantly longer than females under constant favourable temperature, as has been commonly found for other insects (e.g. Kehat & Gordon 1975; Carroll & Quiring 1993). However, high oviposition rate in *B. piniarius* occurs only during the first half of the adult lifespan (Botterweg 1978, Šmits et al. 2001) and prolonged longevity is unlikely to contribute much to overall realised fecundity.

There were no differences in fat and eggs retained after death between females raised at constant normal temperature and females experiencing a short period of low temperature. Females exposed to 10 °C were able to realize all resources as efficiently as females at normal temperature. A relatively small difference in realized fecundity between females experiencing 10 °C and females at normal temperature could be attributed to the fact that more energy was required to tolerate unfavourable conditions and, possibly, to oosorption (e.g. Vogt & Walker 1987).

The effect of delayed mating in combination with low temperature was similar to low temperature alone because of the extremely low oviposition rate. However, delayed mating at the normal temperature resulted in decreased egg fertility because a large proportion of eggs was laid before mating. Some of the unfertilised females started laying eggs the first day after eclosion. A similar response has been observed in other Lepidoptera (Leather et al. 1985; Vickers 1997). However, delayed mating is probably not common in *B. piniarius* under normal weather conditions. Only a small proportion of *B.piniarius* females caught in light traps are unmated (Botterweg 1978) and simulation models showed that 95% of emerging females mate during the first day (Botterweg 1982). In addition, unfertilised eggs are uncommon in the field (Klomp 1966). However, temperatures around 10°C have an adverse effect on *B. piniarius* flight activity (Botterweg 1978), possibly resulting in delayed mating, especially if the low temperature is accompanied by rain or strong wind. This study clearly shows that such weather conditions could affect fecundity, but not egg fertility, as females lay no eggs.

This study has shown that weather can affect *B. piniarius* oviposition behaviour and, consequently, realised fecundity. Depending on the severity and length of unfavourable weather conditions, such as rain and low temperature, the effect could be more or less pronounced. Periods of temperatures below 10 °C occasionally occur during June-July (at the time of *B.piniarius* emergence and oviposition) in the Baltic countries and Scandinavia (data from meteorological stations in Riga and Uppsala). However, the periods of such low temperature are usually short and do not last for more than a week.

This study emphasizes the need to include the knowledge about female behaviour when analysing insect population dynamics (cf. Preszler & Price 1988; Price et al. 1990; Cornell et al. 1998, Šmits et al. 2001). Forecasts concerning the risk of defoliation are often based on female potential fecundity, which may be much higher than realised fecundity. Managers are often faced with the question of whether or not adverse weather conditions during the egg-laying period can significantly modify their risk models. These results indicate that weather conditions must be taken into account because realised fecundity will be reduced if weather is bad during the flight and oviposition period.

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ВЛИЯНИЕ ПОНИЖЕННОЙ ТЕМПЕРАТУРЫ И ЗАПОЗДАЛОГО СПАРИВАНИЯ НА ПЛОДОВИТОСТЬ СОСНОВОЙ ПЯДЕНИЦЫ (*BUPALUS PINIARIUS*)

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Резюме

Неблагоприятные условия погоды во время периода яйцекладки насекомых могут привести к ограниченной возможности откладки яиц. Это в свою очередь может привести к понижению фактической плодовитости. В природе температурные условия могут значительно отклониться от оптимальных для насекомых, но неблагоприятные условия редко длятся продолжительный период времени. Влияние короткого периода (4-5 дней) пониженной температуры (10 °С) и запоздалого спаривания (4 дня) на плодовитость сосновой пяденицы изучалось в лабораторных условиях. Некоторые самки подвергались влиянию пониженной температуры сразу после вылупления, а некоторые через два дня после вылупления. Пониженная температура имела радикальный эффект на поведение самок. Только несколько яиц было отложено при этой температуре. Плодовитость самок, державшихся при температуре 10 °С 4-5 дней была значительно меньше, чем у самок державшихся при температуре 20 °С постоянно. Разница в числе неотложенных яиц и в количестве жира после гибели между вариантами не наблюдалось. Самки с запоздалым спариванием, державшиеся при нормальной температуре, отложили 30% яиц перед оплодотворением, а самки, державшиеся при пониженной температуре, перед оплодотворением отлажили только 0.4% яиц. Эти неоплодотвореные яица нежизнеспособны, и таким образом снижается фактическая плодовитость.

Ключевые слова: *Bupalus piniarius*, откладывание яйц, фактическая плодовитость, температура, запоздалое спаривание