

Effect of Male and Female Age on the Mating Success of the Obliquebanded Leafroller *Choristoneura rosaceana* (Lepidoptera: Tortricidae) Under Different Ecological Conditions

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*The present study was undertaken to test the hypothesis that male and female age, as well as temperature, can affect the mating success of *Choristoneura rosaceana*, given the role that these two factors play in the pheromone biology of this species. In the laboratory, the mating success of females generally declined linearly with age, whereas in males, it increased during the first 3 days and then decreased. The decline in female mating success was more pronounced under warm than cool thermocycles, while the changes observed in males were greater under fluctuating than constant temperature regimes. The onset time of mating was unaffected by male age, however, older females always mated earlier than younger ones, with the advance being more pronounced at cool than warm temperatures. Similar results were also obtained under field conditions. When a single 3-day-old male was provided with 0-, 3-, and 5-day-old females simultaneously, older females obtained mates significantly more often than younger individuals at all temperatures, indicating that calling earlier may afford a reproductive advantage to older females. At both constant temperatures, the time spent mating was longer in older than in younger females, but not under fluctuating thermocycles. Very young and very old males generally spent more time in copula than middle-aged individuals both at constant temperatures and under the warm thermocycle. Under the cool thermocycle, the duration of mating was considerably prolonged at all ages, which could increase the risk of predation.*

KEY WORDS: age and temperature effects; mating success; onset time and duration of mating.

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INTRODUCTION

Age is one of many factors that can influence the mating success of insects. In the majority of studies examining mating success in moths, the age of one sex was varied while that of the other was kept constant (Hirano and Muramoto, 1976; Kanno and Sato, 1978; Proshold *et al.*, 1982; Kiritani and Kanoh, 1984; Swaby *et al.*, 1987; Lingren *et al.*, 1988; Unnithan and Paye, 1991), although there are a few examples where the ages of both partners have been manipulated simultaneously (Outram, 1971; Marks, 1967; Kehat and Gordon, 1977a,b; Bernier-Cardou *et al.*, 1992). In all of the above studies, the experiments were carried out under one single constant temperature regime. However, as temperature can (i) affect the age at which females emit pheromone for the first time and males become responsive to it (Bollinger *et al.*, 1977; Swier *et al.*, 1977; Turgeon and McNeil, 1982; Webster and Cardé, 1982; Dumont and McNeil, 1992) and (ii) influence the diel periodicity of emission and receptivity once the adults have become sexually mature (Cardé *et al.*, 1975; Webster and Cardé, 1982; Turgeon and McNeil, 1983; Delisle and McNeil, 1987a,b), it is not unreasonable to expect that mating success may vary with temperature.

To test this hypothesis, I chose the obliquebanded leafroller (OBL), *Choristoneura rosaceana* (Harris), as the calling behavior and pheromone production of virgin females of this species are known to vary with age and temperature (Delisle, 1992a; Delisle and Royer, 1994), and both factors alter their level of attractiveness under field conditions (Delisle, 1992a,b). In the present study, I examined the OBL mating success as a function of (i) male and female age; (ii) sex ratio, to determine if males accept the first available receptive mates or exhibit some degree of mate choice; and (iii) temperature under laboratory conditions. In addition, I compared the mating success of different-aged, tethered virgin females placed in the field during warm and cool nights of the summer flight when the density of males was not a limiting factor. Furthermore, as Drummond (1984) suggested that mating pairs may be susceptible to predation, data on the onset (laboratory and field) and duration of mating (laboratory) were obtained, as these parameters may influence the degree to which pairs in copula are exposed to predators in nature.

MATERIALS AND METHODS

All insects used in these experiments were obtained from a 1-year-old colony established from field-collected larvae and reared on a pinto bean diet (Shorey and Hale, 1965), at a density of two individuals per cup (Model P100, 28.3 ml; Solo Cup Co., Chicago, IL) at 20°C, 16L:8D, and 65 ± 1% RH. The sexes were separated at the pupal stage, and upon emergence, adults were held individually in 150-cm³ vials containing an 8% sucrose solution. Males and females were maintained in separate growth chambers until they were used.

Male Mating Success in the Laboratory

The mating success of single pairs, using all nine combinations of 0-, 3-, and 5-day-old males and females, was determined for two constant (15 and 20°C) and two fluctuating (warm, summer—25–12°C, $\bar{X} = 19.2^\circ\text{C}$; and cool, fall—17–9°C, $\bar{X} = 14.9^\circ\text{C}$) temperature regimes under a 16L:8D photoperiod and with $65 \pm 1\%$ RH. With the exception of the experiment conducted at 15°C constant (where individuals were transferred to that temperature as mature pupae), all adults were held at 20°C until being transferred, at the appropriate age, to the experimental conditions 5 h before lights-off on the day of testing. The rate of temperature change was 1.0 and 0.5°C/h from the time of transfer under the warm and cool thermocycles, respectively. All pairs, placed in individual 150-cm³ vials, were observed at 30-min intervals from the time of transfer until the beginning of the following photophase. During the scotophase, observations were made using a flashlight covered with a Kodak Wratten No. 29 red gelatin filter. Under each temperature regime, the incidence of mating, the mean onset time of mating (MOTM; expressed as minutes after lights-on), and the mean time spent mating (MTSM; expressed as minutes) were recorded. Under each temperature regime, a minimum of 100 individual pairs was tested for each age combination.

For each temperature regime, the relationship between the age of both sexes and the probability of mating was analyzed using a logistic regression model with the maximum-likelihood ratio (χ^2) serving as a method of estimation. This analysis was performed using the CATMOD procedure of SAS/STAT (SAS Institute, 1990). Orthogonal contrasts (Snedecor and Cochran, 1967) were also used to assess the linear and quadratic effects of both male and female age on the probability of mating under the different temperature regimes: constant temperatures versus thermocycles (T_1), 20 versus 15°C constant (T_2), and warm versus cool thermocycles (T_3). The logistic regression model was then used to calculate polynomial equations.

Data on the MOTM and MTSM (transformed to the naperian logarithm to obtain homoscedasticity) were subjected to analysis of variance [GLM procedure of SAS/STAT (SAS Institute, 1990)] using male and female age (0, 3, and 5 days old for both sexes) and temperature regimes [constant temperatures versus thermocycles (T_1), 20 versus 15°C constant (T_2), warm versus cool thermocycles (T_3)] as main effects. As with mating success, orthogonal contrasts were carried out, and polynomial equations (obtained by multiple regression) determined.

Male Mate Choice

To test whether males showed some degree of mate choice, under each of the four temperature regimes described above, three females (one 0-, 3-, and 5-day-old individual, each with a small area of the anterior wing removed to

identify its age category) were placed in a 300-cm³ vial with a single 3-day-old male 5 h prior to lights-off. Observations were made at 30-min intervals, and following mating, the pair was left undisturbed for approximately 1 h before being removed to determine, by the presence of a spermatophore in the bursa, which female was mated. For each temperature regime, the experiment was repeated at least 20 times.

The numbers of matings obtained by the different-aged females, as well as the numbers of unsuccessful trials, were arranged in a $4 \times 2 \times 2$ contingency table, using as categorical variables (i) mating partner (none or day 0, 3, or 5 female) and (ii) two special codings for the effect of temperature: (a) temperature regime (constant and fluctuating) and (b) the level of temperature (warm and cool). A sequence of hierarchical log-linear models was adjusted and successive goodness-of-fit statistics (χ^2) were computed and compared with the appropriate chi-square distribution (Agresti, 1984), using the BMDP4F procedure from the BMDP Statistical Software Manual (Dixon, 1990).

Mating Success in the Field

The mating success of 0-, 3-, and 5-day-old virgin females was tested in a deciduous forest near Quebec City. Laboratory individuals were reared and maintained at 20°C constant under a 16L:8D photoperiod (lights-on at 0500 and lights-off at 2100). In the midafternoon (1500), on the day of testing, a minimum of 11 tethered females from each of the three age classes was randomly attached to branches of randomly chosen host trees, spaced 8 m apart. There was only one female per tree. A 15-cm fishing line, attached to a spot devoid of scales on the thorax of the female with a nontoxic glue, was used to tether each individual. Females were observed every 30 min between 1600 and 2400 (EST) to determine the time of mating and all individuals were left in the field until 0700 the following morning. Females were brought back to the laboratory and dissected to determine, by the presence of a spermatophore in the bursa, if some individuals mated between the time observations ceased and the time they were collected. This experiment was repeated on 3 warm and 3 cool nights during the summer flight period.

The numbers of mated and unmated females, as well as the numbers of missing data points (death from predation or escape), were arranged in a $3 \times 3 \times 2$ contingency table, using female age (0, 3, and 5 days old), status (mated, unmated, and missing), and temperature (warm and cool) as the three categorical variables. The data were analyzed with the same tests used in the laboratory mate choice experiment.

Data on the MOTM were subjected to an analysis of variance, with female age (0, 3, and 5 days old) and temperature (warm and cool) as main effects. As for each temperature condition, the experiment was repeated on 3 nights, the

effect of nights (nested within temperature) was also taken into account in the model and used as the *F*-test denominator for temperature effects (Rowell and Walters, 1976). Orthogonal contrasts were also performed to assess the linear and quadratic trends of female age. For both temperature regimes, polynomial equations that best described the relationship between MOTM and female age were determined.

RESULTS

Mating Success in the Laboratory

The probability of mating decreased linearly with age in females, while for males it increased from day 0 to day 3 and then decreased (Table I). These quite opposing trends obviously influenced the overall level of mating seen for any given age combination (Table I) and explains the significant interaction observed between male and female age (Table II), following the best-fitting logistic regression model ($\chi^2 = 32.44$, $df = 25$, $P = 0.1450$). However, the *F* * *M* interaction was less important than the effects of either male or female age alone and was independent of temperature, as the interaction (*T* * *F* * *M*) was not significant (Table II).

The relative importance of male and female age in OBL mating success

Table I. The Observed Probability of Mating of Single Pairs, Using All Age Combinations (0, 3, and 5 Days Old) of *Choristoneura rosaceana* Females (*F*) and Males (*M*) Under a 16L:8D Photoperiod at 20 and 15°C Constant, as Well as Under Warm and Cool Fluctuating Temperatures

Age	<i>F</i> ₀	<i>F</i> ₃	<i>F</i> ₅	$\bar{X}_{(M)}$	<i>F</i> ₀	<i>F</i> ₃	<i>F</i> ₅	$\bar{X}_{(M)}$
Constant								
20°C				15°C				
<i>M</i> ₀	0.30	0.15	0.14	0.19	0.07	0.02	0.04	0.04
<i>M</i> ₃	0.58	0.38	0.25	0.41	0.20	0.18	0.18	0.19
<i>M</i> ₅	0.45	0.33	0.32	0.36	0.36	0.32	0.30	0.33
$\bar{X}_{(F)}$	0.44	0.29	0.24		0.21	0.17	0.17	
Fluctuating								
Warm				Cool				
<i>M</i> ₀	0.28	0.10	0.07	0.15	0.22	0.10	0.05	0.12
<i>M</i> ₃	0.68	0.48	0.39	0.51	0.40	0.44	0.33	0.39
<i>M</i> ₅	0.43	0.48	0.25	0.36	0.29	0.21	0.27	0.26
$\bar{X}_{(F)}$	0.46	0.34	0.24		0.32	0.27	0.23	

Table II. The Effect of Temperature (T_1 , T_2 , T_3), Female Age (F), and Male Age (M), as Well as the Interactions Between the Different Factors, on the Probability of Mating of Single Pairs of *Choristoneura rosaceana* Adults Maintained Under a 16L:8D Photoperiod, Using a Logistic Regression

Source of variation	df	χ^2	P
Intercept	1	681.99	0.0000
Temperature			
T_1 : constant vs fluctuating	1	10.13	0.0015
T_2 : 20 vs 15°C constant	1	57.89	0.0000
T_3 : warm vs cool fluctuating	1	20.62	0.0000
Female age			
Linear (F)	1	79.29	0.0000
Male age			
Linear (M)	1	165.69	0.0000
Quadratic (M^2)	1	89.54	0.0000
Female age * Male age			
$F * M$	1	12.36	0.0004
Temperature * female age			
$T_3 * F$	1	7.39	0.0066
Temperature * male age			
$T_2 * M$	1	19.80	0.0000
$T_1 * M^2$	1	23.05	0.0000
Maximum-likelihood ratio (G)	25	32.44	0.1450

varied with temperature (Table I), as indicated by the significant interactions ($T * F$) and ($T * M$) (Table II). In females, the linear decline in mating success with age was slightly more pronounced under warm than under cool thermocycles ($T_3 * F$), as young females did better at warm than at cool fluctuating temperatures. Older females did equally well in both environments. In males, the change in mating success with age was more pronounced at 15 than at 20°C constant, as the success of young individuals was significantly lower at 15 than at 20°C constant, while older males did equally well under both temperature regimes ($T_2 * M$). Furthermore, the quadratic effect of male age on mating success was significantly greater at fluctuating than constant temperatures ($T_1 * M^2$). This was due to the greater success of day 3 males at fluctuating than constant temperatures, while day 0 and day 5 males were less successful regardless of the temperature regime.

The probability of mating (\hat{Y}) obtained in response to OBL female (F) and male (M) age at each temperature regime (Table I) can best be described by the following polynomial equations:

$$\hat{Y}_{(20^\circ\text{C})} = -0.6421 - 0.2711F + 0.3794M + 0.0369FM - 0.0637M^2 \quad (1)$$

$$\hat{Y}_{(15^\circ\text{C})} = -2.3393 - 0.2711F + 0.6632M + 0.0369FM - 0.0637M^2 \quad (2)$$

$$\hat{Y}_{(warm)} = -1.0184 - 0.3383F + 1.1101M + 0.0369FM - 0.1853M^2 \quad (3)$$

$$\hat{Y}_{(cool)} = -1.897 - 0.2039F + 1.1106M + 0.0369FM - 0.1853M^2 \quad (4)$$

after backtransformation using the expression $\hat{Y} = [\exp \hat{Y}/1 + \exp \hat{Y}]$.

The time at which mating began (MOTM) was strongly influenced by temperature (Fig. 1), with mating occurring significantly earlier under cool than under warm temperatures, at both constant and fluctuating regimes (Table III). However, the significant advance in the MOTM was more important under fluctuating (~2-h) than constant (~1-h) temperature regimes, for all ages. The MOTM was also strongly influenced by female age (both linear and quadratic effects; Table III), with day 3 and day 5 females initiating mating at the same time but significantly earlier than newly emerged individuals. These trends were similar under all temperature regimes, as no significant interactions were found between temperature and female age ($T * F$). In contrast, the effect of male age (M) alone or in combination with either temperature ($T * M$), female age ($F * M$) or both factors ($T * F * M$) had no significant influence on the MOTM (Table III). Thus, for each temperature regime, the relationship between female (F) age and the MOTM (\hat{Y}) can best be described by the following polynomial equations:

$$\hat{Y}_{(20^\circ C)} = \exp (6.99 - 0.02F + 0.003F^2) \quad (5)$$

$$\hat{Y}_{(15^\circ C)} = \exp (6.95 - 0.02F + 0.003F^2) \quad (6)$$

$$\hat{Y}_{(warm)} = \exp (6.94 - 0.02F + 0.003F^2) \quad (7)$$

$$\hat{Y}_{(cool)} = \exp (6.80 - 0.02F + 0.003F^2) \quad (8)$$

which were used to simulate the response curves shown in Fig. 1.

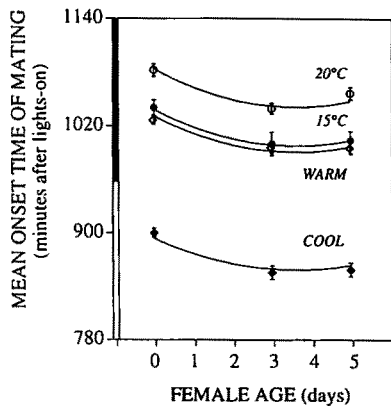


Fig. 1. Predicted (lines) and observed (symbols) backtransformed values of the mean onset time of mating (\pm SE) of different-aged (0-, 3-, and 5-day-old) *Choristoneura rosaceana* females under a 16L:8D photoperiod at 20 and 15°C constant, as well as under warm and cool fluctuating temperature regimes. The photophase and scotophase are indicated by the white and black bars on the Y axis, respectively.

Table III. The Mean Square (MS) and the Level of Significance (*P*) of Each Orthogonal Contrast Used to Test for Differences in the Mean Onset Time of Mating (MOTM) and the Mean Time Spent Mating (MTSM) of Single Pairs of *Choristoneura rosaceana* Adults Under a 16L:8D Photoperiod in Response to Temperature Regimes (T_1 , T_2 , T_3), Female Age (*F*), Male Age (*M*), and the Interactions Between the Different Factors

Source of variation	df	MOTM		MTSM	
		MS	<i>P</i>	MS	<i>P</i>
Temperature	3	1.129	0.0001	2.005	0.0001
T_1 : constant vs fluctuating	1	1.396	0.0001	1.245	0.0001
T_2 : 20 vs 15°C constant	1	0.073	0.0001	0.154	0.1255
T_3 : warm vs cool fluctuating	1	1.639	0.0001	0.524	0.0001
Female age	2	0.095	0.0001	0.193	0.0527
Linear (<i>F</i>)	1	0.148	0.0001	0.251	0.0502
Quadratic (F^2)	1	0.020	0.0057	0.185	0.0923
Temperature * female age	6	0.005	0.0722	0.141	0.0443
$T_1 * F$	1	0.004	0.2161	0.277	0.0397
$T_1 * F^2$	1	0.000	0.6937	0.119	0.1771
$T_2 * F$	1	0.000	0.5842	0.045	0.4041
$T_2 * F^2$	1	0.007	0.1061	0.093	0.2306
$T_3 * F$	1	0.008	0.0736	0.193	0.0862
$T_3 * F^2$	1	0.005	0.1510	0.059	0.3421
Temperature * female age	6	—	—	0.141	0.0443
Constant * <i>F</i>	1	—	—	0.480	0.0068
Fluctuating * <i>F</i>	1	—	—	0.000	0.9415
Male age	2	0.006	0.0896	0.433	0.0014
Linear (<i>M</i>)	1	0.010	0.0545	0.121	0.1741
Quadratic (M^2)	1	0.008	0.0772	0.866	0.0003
Temperature * male age	6	0.000	0.2557	0.079	0.2971
$T_1 * M$	1	0.000	0.8012	0.009	0.7154
$T_1 * M^2$	1	0.008	0.0756	0.008	0.7303
$T_2 * M$	1	0.007	0.0949	0.007	0.7393
$T_2 * M^2$	1	0.000	0.5645	0.064	0.3227
$T_3 * M$	1	0.004	0.1978	0.036	0.4575
$T_3 * M^2$	1	0.000	0.9685	0.384	0.0154
Temperature * male age	6	—	—	0.079	0.2971
Constant * M^2	1	—	—	0.453	0.0086
Warm fluctuating * M^2	1	—	—	1.043	0.0001
Cool fluctuating * M^2	1	—	—	0.000	0.9522
Female age * male age	4	0.002	0.5161	0.132	0.0883
$F * M$	1	0.000	0.5869	0.002	0.8705
$F * M^2$	1	0.001	0.5267	0.010	0.7029
$F^2 * M$	1	0.005	0.1387	0.499	0.0058
$F^2 * M^2$	1	0.003	0.3094	0.049	0.3880
Temperature * female age * male age	12	0.002	0.8579	0.064	0.4696
$T_1 * F * M$	1	0.000	0.5963	0.007	0.7390
$T_1 * F * M^2$	1	0.000	0.7551	0.048	0.3892
$T_1 * F^2 * M$	1	0.004	0.2348	0.035	0.4645
$T_1 * F^2 * M^2$	1	0.002	0.4080	0.005	0.7806
$T_2 * F * M$	1	0.000	0.9456	0.012	0.6650
$T_2 * F * M^2$	1	0.000	0.6097	0.004	0.8104
$T_2 * F^2 * M$	1	0.000	0.6004	0.105	0.2055

Table III. Continued

Source of variation	df	MOTM		MTSM	
		MS	P	MS	P
$T_2 * F^2 * M^2$	1	0.001	0.5104	0.030	0.4966
$T_3 * F * M$	1	0.000	0.8390	0.053	0.3679
$T_3 * F * M^2$	1	0.000	0.6860	0.006	0.7605
$T_3 * F^2 * M$	1	0.005	0.1737	0.369	0.0177
$T_3 * F^2 * M^2$	1	0.001	0.5104	0.012	0.6654
Temperature * female age * male age	12	—	—	0.064	0.4696
Constant * $F^2 * M$	1	—	—	0.305	0.0309
Warm fluctuating * $F^2 * M$	1	—	—	0.015	0.6296
Cool fluctuating * $F^2 * M$	1	—	—	0.500	0.0058
Error IV	955; 912	0.003		0.065	

The influence of male and female age on the MTSM (Table IV) was similar at both 20 and 15°C constant but differed significantly between warm and cool thermocycles, as well as between fluctuating and constant temperature regimes (Table III). Older OBL females spent more time in copula than younger individuals (Table IV), but the effect was significant only under constant temperature regimes (constant * F) (Table III). In contrast, the duration of mating was shorter when OBL females were paired with middle-aged rather than younger or older males under constant temperatures (constant * M^2), as well as under the warm thermocycle (warm fluctuating * M^2). The MTSM increased linearly with male age and was more pronounced when mating occurred with 3-day-old females and at constant temperatures or under the cool thermocycle (constant * $F^2 * M$). The influence of male (M) and female (F) age on the MTSM (\hat{Y}) under the different temperature regimes (Table IV) can best be expressed by the following polynomial equations:

$$\hat{Y}_{(20^\circ\text{C})} = \exp (5.4090 - 0.0288F + 0.01F^2 - 0.0759M + 0.0145M^2 + 0.0182MF - 0.0037MF^2) \tag{9}$$

$$\hat{Y}_{(15^\circ\text{C})} = \exp (5.4090 - 0.0288F + 0.01F^2 - 0.0759M + 0.0145M^2 + 0.0182MF - 0.0037MF^2) \tag{10}$$

$$\hat{Y}_{(\text{warm})} = \exp (5.4085 - 0.0897M + 0.0185M^2) \tag{11}$$

$$\hat{Y}_{(\text{cool})} = \exp (5.7088 - 0.1436 F + 0.0296F^2 - 0.0175M + 0.0538MF - 0.0111MF^2) \tag{12}$$

Table IV. The Observed Mean Time Spent Mating (MTSM \pm SE) by Single Pairs of All Age Combinations (0, 3, and 5 Days Old) of *Choristoneura rosaceana* Females (*F*) and Males (*M*) Under a 16L:8D Photoperiod at 20 and 15°C Constant, as Well as Under Warm and Cool Fluctuating Temperatures

Age	F_0	F_3	F_5	$\bar{X}_{(M)}$	F_0	F_3	F_5	$\bar{X}_{(M)}$
Constant								
20°C								
M_0	240.9 \pm 14.3	237.4 \pm 22.4	272.1 \pm 19.7	249.7 \pm 10.3	238.7 \pm 11.0	180.0 \pm 1.0	272.1 \pm 35.7	228.7 \pm 16.0
M_3	196.6 \pm 9.0	216.0 \pm 14.5	237.5 \pm 16.1	216.0 \pm 7.2	204.9 \pm 6.2	209.4 \pm 10.3	226.3 \pm 7.1	213.4 \pm 4.8
M_5	221.1 \pm 10.7	240.5 \pm 12.5	246.4 \pm 15.7	235.7 \pm 7.4	218.0 \pm 4.9	225.4 \pm 9.9	221.1 \pm 7.4	221.5 \pm 7.4
$\bar{X}_{(F)}$	218.8 \pm 9.0	231.0 \pm 14.5	251.6 \pm 16.1		220.1 \pm 6.2	204.1 \pm 10.3	240.6 \pm 7.6	
15°C								
Fluctuating								
Warm								
M_0	219.7 \pm 9.6	245.5 \pm 24.6	242.9 \pm 38.1	235.8 \pm 9.9	324.2 \pm 20.4	242.2 \pm 32.3	299.0 \pm 76.5	286.3 \pm 18.3
M_3	198.0 \pm 5.1	204.4 \pm 4.8	202.4 \pm 6.5	201.6 \pm 3.1	292.8 \pm 17.2	287.6 \pm 10.4	275.7 \pm 16.2	285.3 \pm 8.4
M_5	221.2 \pm 7.6	225.3 \pm 8.1	230.3 \pm 11.3	225.5 \pm 4.9	280.0 \pm 13.0	306.7 \pm 20.0	271.8 \pm 14.2	285.8 \pm 8.8
$\bar{X}_{(F)}$	212.7 \pm 5.1	224.4 \pm 4.8	224.5 \pm 6.5		298.4 \pm 17.2	277.5 \pm 10.3	281.9 \pm 16.2	
Cool								

Table V. The Number of Times that a Single 3-Day-Old *Choristoneura rosaceana* Male Mated with No, 0-, 3-, or 5-Day-Old Females When Provided with Three Females Simultaneously Under a 16L:8D Photoperiod at 20 and 15°C Constant and Under Warm and Cool Fluctuating Temperatures (The Best-Fitting of a Log-Linear Model Yields the Predicted Values Given in Parentheses)

Regime	T	Mating partners				Total
		None	F ₀	F ₃	F ₅	
Constant	20°C	38 (40.8)	6 (4.7)	20 (19.1)	19 (18.4)	83
	15°C	29 (29.0)	6 (3.3)	9 (13.6)	15 (13.1)	59
Fluctuating	Warm	6 (9.8)	1 (1.1)	7 (4.6)	6 (4.4)	20
	Cool	49 (42.3)	1 (4.9)	21 (19.8)	15 (19.1)	86
Total		122 (121.9)	14 (14.0)	57 (57.1)	55 (55.0)	248
%		49.2	5.6	23.0	22.2	

Male Mate Choice

Successful matings occurred in 50% of the trials (126/248) (Table V), when a single 3-day-old male had the choice to mate with 0-, 3-, or 5-day-old virgin OBL females. The log-linear analysis shows that the best-fitting model yields the predicted values given in parentheses beside the observed frequencies in Table V ($\chi^2 = 14.24$, $df = 9$, $p = 0.1139$). This model assumes that the frequency of mating differed significantly with female age (none, 0, 3, and 5 days old); however, the adequacy of the model was verified when the association between mating partner and temperature ($M * T$), as well as mating partner and regime ($M * R$), was not included. These results were the same, irrespective of whether the temperature was warm or cool or the regime constant or fluctuating. A t test ($t_{\alpha/2} = 1.96$) on the parameters of the model indicates that day 3 ($|t_0 = 5.78| > t_{\alpha/2}$) and day 5 ($|t_0 = 5.62| > t_{\alpha/2}$) females (22% each) mated significantly more than day 0 individuals (6%).

Mating Success in the Field

The proportion of individuals that successfully mated, remained unmated, or disappeared under field conditions (Table VI) was unaffected by female age within each temperature category based on the best log-linear model ($\chi^2 = 12.42$, $df = 8$, $P = 0.1398$). However, there was a significant association between status and temperature ($S * T$). A comparison of the frequencies, using a t test ($t_{\alpha/2} = 1.96$) on the parameters of the model, indicated that the proportion of females mating is similar at both temperatures ($t_0 = 1.10 < t_{\alpha/2}$), but more females remain unmated on cool nights ($|t_0 = 3.88| > t_{\alpha/2}$) and more individuals are missing on warm nights ($|t_0 = 10.87| > t_{\alpha/2}$).

Table VI. The Number of Different-Aged (0-, 3-, and 5-Day-Old) Tethered *Choristoneura rosaceana* Females that Were Mated, Unmated, or Found Missing on Warm and Cool Nights Under Field Conditions (The Best-Fitting of a Log-Linear Model Yields the Expected Values Given in Paentheses)

Temperature	Age	Status			Total
		Mated	Unmated	Missing	
Warm	F_0	36 (31.0)	3 (5.3)	2 (4.7)	41
	F_3	30 (31.0)	7 (5.3)	4 (4.7)	41
	F_5	27 (31.0)	6 (5.3)	8 (4.7)	41
	Total	93 (93.0)	16 (15.9)	14 (14.1)	123
	%	75.6	13.0	11.4	
Cool	F_0	25 (25.8)	13 (10.6)	1 (2.6)	39
	F_3	26 (26.4)	12 (10.7)	2 (2.7)	40
	F_5	27 (25.8)	7 (10.6)	5 (2.6)	39
	Total	78 (78.0)	32 (32.0)	8 (7.9)	118
	%	66.1	27.1	6.8	

On the other hand, the MOTM in the field was strongly influenced by female age and temperature (Fig. 2). Day 3 and day 5 females initiated mating earlier than day 0 individuals during both warm and cool nights (Table VII, Fig. 2), with no significant interaction found between temperature and female age (Table VII). Furthermore, irrespective of female age, mating occurred nearly 2 h earlier on cool than on warm nights (Fig. 2) and these results agree with those obtained under controlled laboratory conditions (Table III, Fig. 1). For each temperature condition, the best relationship between female age (F) and

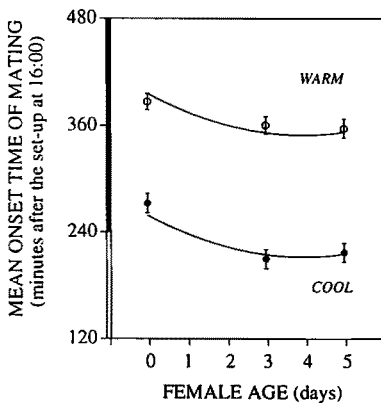


Fig. 2. Predicted (lines) and observed (symbols) values of the mean onset time of mating (\pm SE) of different-aged (0-, 3-, and 5-day-old) tethered *Choristoneura rosaceana* virgin females on warm and cool nights during summer flight. The photophase and scotophase are indicated by the white and black bars on the Y axis, respectively.

Table VII. The Mean Square (MS) and the Level of Significance (*P*) of Each Orthogonal Contrast Used to Test for Differences in the Mean Onset Time of Mating (MOTM) of *Choristoneura rosaceana* Virgin Females in Response to Temperature, Nights Nested in Temperature, Female Age, and the Interactions Between the Two Factors

Source of variation	df	MS	<i>P</i>
Temperature	1	835214.8	0.0001
Nights (in temperature)	4	38447.7	0.0001
Female age	2	34295.4	0.0001
Linear (<i>F</i>)	1	59615.7	0.0001
Quadratic (<i>F</i> ²)	1	13222.4	0.0400
Temperature * age	2	5058.0	0.1971
Error IV	161	3082.7	

the MOTM (\bar{Y}) can be expressed using the following polynomial equations:

$$\hat{Y}_{(warm)} = 396.4 - 23.8F + 3.02F^2 \tag{13}$$

$$\hat{Y}_{(cool)} = 259.0 - 23.8F + 3.02F^2 \tag{14}$$

which were used to generate the response curves seen in Fig. 2.

While the mating success of different-aged females did not differ overall under the different ecological conditions (Table VI), the hourly cumulative incidence of mating (Fig. 3) indicated that more day 3 and day 5 females mated early in the night than newly emerged ones, and this pattern was more pronounced on cool than on warm nights.

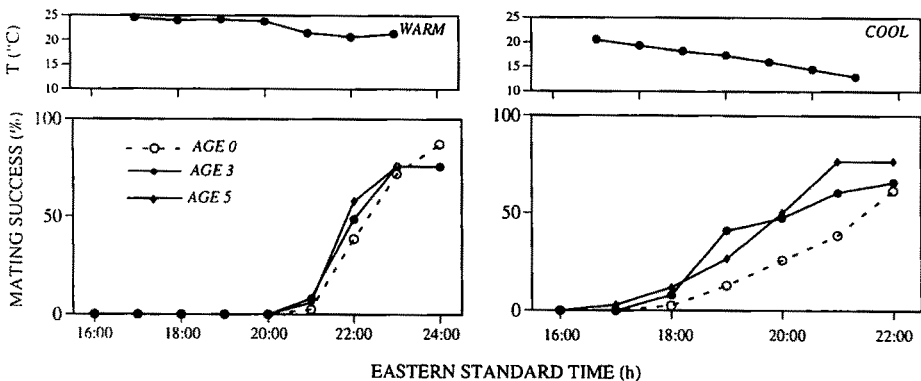


Fig. 3. The hourly cumulative incidence of mating of different-aged (0-, 3-, and 5-day-old) tethered *Choristoneura rosaceana* virgin females on warm and cool nights during summer flight. The standard errors of each mean hourly temperature are too small to be seen on the upper graphs.

DISCUSSION

The majority of studies that have examined the effect of age on mating success has either varied the age of one sex while maintaining the age of the other constant (Hirano and Muramoto, 1976; Kanno and Sato, 1978; Proshold *et al.*, 1982; Kiritani and Kanoh, 1984; Swaby *et al.*, 1987; Unnithan and Paye, 1991) or used male-female pairs of the same age (Kanno and Sato, 1978; Henneberry and Clayton, 1983; Seol *et al.*, 1986; Jackai *et al.*, 1990; Unnithan and Paye, 1991). However, the mating success of an individual not only is dependent upon its own age but can also be significantly affected by the age of its partner (Outram, 1971; Marks, 1976; Kehat and Gordon, 1977a,b; Bernier-Cardou *et al.*, 1992). It is evident in the case of OBL that the age of both partners will determine the mating success under all temperature conditions (Table I). For example, the success of newly emerged females increases with the male age, while younger males do better if they encounter a newly emerged female.

The mating success of female moths generally declines with age (Outram, 1971; Swaby *et al.*, 1987; Unnithan and Paye, 1991), which may be the result of reduced pheromone titers and an increasing proportion of time spent laying eggs as virgin females age (Giebultowicz *et al.*, 1990; Teal *et al.*, 1990). The observed decline in OBL female mating success could be associated with a lower pheromone production (Delisle and Royer, 1994) but, in this case, not with oviposition activity, for in all experiments, I used only females that did not lay eggs.

In male Lepidoptera, increased mating success with age has been associated with several interrelated factors, including the timing of emergence and sperm release. In *Heliothis virescens* (F.), the release of sperm occurs only in the first half of the photophase, with "lights-on" serving as the cue. Thus, males emerging several hours after lights-on will be unable to store sufficient sperm to mate the following night (Henneberry and Clayton, 1985; Proshold, 1991). A similar system has also been reported for pink bollworm males (LaChance *et al.*, 1977; Henneberry and Clayton, 1983). Male responsiveness to female sex pheromone is another factor known to change with age, generally increasing in the days following emergence (Shorey *et al.*, 1968; Bollinger *et al.*, 1977; Kanno and Sato, 1978; Baker and Cardé, 1979; Szócs and Tóth, 1979; Tóth, 1979; Turgeon and McNeil, 1983; Dumont and McNeil, 1992). Furthermore, Shorey *et al.* (1968) reported a close relationship between sperm storage and the onset of male responsiveness in several noctuid species: males containing eupyrene sperm in the duplex at the time of emergence were more likely to respond to pheromone and mate at a younger age than those that did not. Age-related changes in the amount of male pheromone produced have been conclusively demonstrated in at least two butterfly species, *Pieris melete* Ménériès (Kuwahara, 1979) and

Thymelicus lineola (Ochsenheimer) (Pivnick *et al.*, 1992), and one moth, *Pseudaletia unipuncta* (Haw.) (Fitzpatrick *et al.*, 1989). Recently emerged males release considerably less pheromone than older individuals and are less attractive to females. The effect of age on the onset of sperm release and storage, the responsiveness of males to the sex pheromone, and the possible release of male scent substances, as well as how these factors influence the mating success of the OBL, merit further consideration, especially as the OBL is a protandrous species.

However, it is evident from the results of this study that the effect of male and female age on mating success is markedly affected by ambient temperature conditions (Table II). Temperature is known to influence male maturation and thus the age at which adults become sexually mature (Bollinger *et al.*, 1977; Turgeon and McNeil, 1982; Webster and Cardé, 1982; Dumont and McNeil, 1992), and this would explain why there was a more pronounced linear increase in mating success of males with age at 15 than at 20°C (Tables I and II). Bollinger *et al.* (1977) showed that *Trichoplusia ni* (Hübner) males held at 15°C during both pupal and adult stages exhibit maximal responsiveness to pheromones 4 days later than those held at 20°C. Similar delays in the onset of male receptivity have been reported for *P. unipuncta* for males held at cooler temperatures (Dumont and McNeil, 1992). Furthermore, Riemann and Thorson (1978) showed that the number of sperm bundles released from the testis into the upper vasa deferentia by *Anagasta kuehniella* (Zeller) males was three to four times less at 17 than at 27°C, with no sperm being released at temperatures below 12°C. However, in this species they reported that the inhibitory effect of temperature on sperm production did not affect the ability of males to mate.

It is very clear from data obtained under the two thermocycles and at 20°C constant (when the physiological state of development at the time of testing was the same) that the curvilinear increase in male mating success with age was significantly greater under cycling than constant temperature regimes (Table I), possibly due to a greater sensitivity of males to the female sex pheromone. In the case of females, the adverse effect of aging on the mating success was less evident under the cooler than the warmer thermocycle (Table I). This agrees with the field observation that older females, relative to younger individuals, attract more males during the fall than the summer flight period (Delisle, 1992a). Whether this is associated with male sensitivity and/or release of pheromone by the female remains to be determined.

The results obtained under constant conditions would indicate that the best age combination for the mating success of *C. rosaceana* would be young females with old males. However, under the cycling temperatures, which more closely reflect field conditions, the best effective age combination was with newly emerged females and middle-aged males, which is not particularly surprising when one considers the biology of the OBL: males emerge several days before

females (J. Delisle, unpublished data) and maximum pheromone production occurs in newly emerged females (Delisle and Royer, 1994). Similar relationships between life history and the optimal age for mating success also exist for the other species where the combined effect of male and female age on mating success was examined. In *Choristoneura fumiferana* (Clem.), mating success also decreased with female age and increased with male age (Outram, 1971; Bernier-Cardou *et al.*, 1992). As in the case of OBL, *C. fumiferana* is a protandrous species (Smith, 1953) and its females produce less pheromone as they age (Grant *et al.*, 1982). In the noctuid, *Spodoptera littoralis* (Boisd.), the mating success of both sexes increased with age, which is consistent with males emerging after females and female attractiveness taking several days to reach a maximum level (Kehat and Gordon, 1977b).

It has been suggested that the advance in the onset time of calling with age in lepidopteran species is an adaptation that permits older females to increase their chances of attracting mates before younger females start calling (Swier *et al.*, 1977; Turgeon and McNeil, 1982; Webster and Cardé, 1982). During the peak of the summer flight, day 3 and day 5 tethered females mated significantly earlier than day 0 individuals, with the effect being more pronounced on cool than on warm nights (Fig. 3). In addition, older OBL females had the highest incidence of mating under cool conditions (Fig. 3), although overall mating success did not differ significantly with age. This is not unexpected, as the experiment was carried out during the peak of the summer flight when the sex ratio was male biased and minimum temperatures never went below the threshold for male flight (13°C) (Delisle, 1992b). However, even at high male densities, the availability of potential mates for young females, which call later in the night (Cardé *et al.*, 1975; Webster and Cardé, 1982; Turgeon and McNeil, 1983; Delisle and McNeil, 1987a,b), would be reduced if temperatures declined below the threshold for male flight activity. For example, if a rapid drop in temperature occurred at sunset (2000) under cool conditions (Fig. 3), thereby reducing male activity, a significantly higher proportion of older females would have mated than younger individuals. Furthermore, if the number of available males is limited, then older females would be advantaged, as the results from choice experiments indicate that OBL males generally accept the first available receptive female (Table V).

Drummond (1984) suggested that, due to their limited mobility, mating pairs would be vulnerable to predation. While there was a slight increase in the duration of mating with female age at both constant temperatures, this was not the case under fluctuating temperature regimes (Table III). Younger females, which start mating later in the scotophase than older individuals, would be most affected by declining temperatures and this would counterbalance the effect of age on mating duration. Male age also influenced the duration of mating, which was longer when females mated with very young or old males at both constant

temperatures and under the warm thermocycle. In contrast, the duration of mating was considerably prolonged under the cool thermocycle for all age combinations (Table IV), suggesting that under field conditions, the risk of predation during copulation might be higher at cool than warm temperatures. However, this assumes that the activity of predators is independent of temperature. This is unlikely, as the only observed acts of predation involved a presently unidentified spider, and being a poikilotherm, it would be affected by temperature conditions. Additional studies under different ecological conditions are necessary to quantify the impact of predation, on both calling females and mating pairs, to determine if mortality is affected by adult age and the associated changes in the time and duration of mating.

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