Seasonal Changes in Adult Longevity and Pupal Weight of the Nantucket Pine Tip Moth (Lepidoptera: Tortricidae) with Implications for Interpreting Pheromone Trap Catch

CHRISTOPHER ASARO[1] AND C. WAYNE BERISFORD

Department of Entomology, 413 Biological Sciences Building, University b(Georgia, Athens, GA 30602

Environ. Entomol. .30(6): 999-1005 (2001)

ABSTRACT Pheromone trap catches of the Nantucket pine tip moth, *Rhyacioniafhtstrana* (Cornstock), are often much higher during the first generation as compared with later generations, regardless of population density or damage levels. One hypothesis proposed to explain this phenomenon is reduced adult longevity during summer due to high temperatures. In this study, adult male and female moths placed in containers in the field during each generation showed significantly shorter life spans during the summer months compared with spring. Life spans were inversely related to the average number of daily degree-days accumulated during the investigations. In the laboratory, adult male moths under varying temperatures and constant humidity showed life spans similar to those observed in the field. Adult male moths that were provided with a sugar water solution in the laboratory did not have significantly longer life spans than those without. Male and female pupal weights showed little variation between generations and sites, and no observable changes in pupal weights occurred during the overwintering period. Some differences in female pupal weight between generations were found at some sites but these differences were not correlated with differences in adult life span. Temperature appeared to be the predominant factor affecting adult moth life span between generations, although other environmental and physiological factors may be important. An understanding of the lower trap catches for *R. frustrana* during summer may have important implications for using pheromone traps to predict population levels.

KEY WORDS *Rhyacionia frustrana,* adult longevity, pupal weight, pheromone trap catch

THE NANTUCKET PINE tip moth, *Rhyacionia frustrana* (Comstock), is a common pest of intensively managed pines throughout the southeastern United States (Berisford 1988). Pheromone traps are an important tool for monitoring and managing this insect (Berisford 1974, Gargiullo et al. 1985, Fettig et al. 2000). However, the full potential of these traps has been limited by an inability to associate trap catch with tip moth density or damage. One difficulty is that trap catches for this multivoltine insect are typically lower during the summer compared with the first adult emergence period in spring regardless of population density or damage levels (Asaro and Berisford 2001, Canalos and Berisford 1981, Berisford et al. 1992, Fettig and Berisford 1999). The causes of this predictable drop in trap catch during summer are unknown. One hypothesis is that adult life span decreases during the summer due to the physiological stress experienced during high temperatures. If adult males have shorter lives, there would be a proportional drop in the mean daily population, which would result in lower trap catches.

Adult tip moths oviposit on needles and shoots of the host tree. Upon hatching, first instars mine needles, while second instars feed at needle or bud axils, forming a characteristic silk tent covered with resin. Subsequent instars (3-5) feed inside buds and shoots and ultimately pupate inside the dead shoot. Pupae are the overwintering stage of this insect (Berisford 1988). Three tip moth generations occur in the Georgia Piedmont (Fettig et al. 2000). Adult emergence of the first (spring) generation normally occurs from late February to late April. Second and third generation adults (the 'summer' generations) generally emerge during June and August, respectively.

Few studies have explored the effects of weather variables on pheromone trap catch (Jönsson and Anderbrant 1993). Comeau et al. (1976) studied the influence of temperature on the diel periodicity in trap catch of six lepidopteran species. Byers and Löfqvist (1989) studied the effects of ambient temperature on the trap catch of *Ips typographies* (L.) (Coleoptera: Scolytidae). Pitcairn et al. (1990) examined the influence of different weather variables on trap catch of codling moths, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae). Other studies have examined the effects of wind speed on trap catch of *Spodoptera litura* (F.) (Lepidoptera: Noctuidae) (Nakamura and Kawasaki 1984) and different bark beetles (Coleoptera: Scolytidae) (Byers et al. 1989). Webb and Berisford (1978) showed that low daytime temperatures induced early flight by R. *frustrana.*

---

[1] E-mail:casaro@arches.usa.edu

A number of studies have demonstrated shorter life spans of adult insects with increasing temperature. Adult female longevity of the soybean looper, *Pseudcy\)lusia includem* (Walker) (Lepidoptera: Geometridae) was shown to decrease linearly as temperature increased (Mason and Mack 1984). Bari and Lange (1980) reported reduced fecundity and adult longevity of the artichoke plume moth, *Platyptilia carduidactyla* (Riley) (Lepidoptera: Pterophoridae), at higher temperatures. Moscajdi et al. (1981) 4*^{0N}ye.d that adult female longevity of the velvetbean cater*pillar, *Anticarsia gemmatalis* Hiibner (Lepidoptera: Noctuidae), decreased with increasing temperatures. A similar trend Was demonstrated for the New Zealand flower thrips *Thrips obscuratus* (Crawford) (Thysanoptera: Thripidae) (Teulon and Penman 1991) and the Swain jack pine sawfly, *Neodiprion swainei* Middleton (Hymenoptera: Diprionidae) (Pilon 1966). However, in none of these studies were the life spans of different generations of the same multivoltine insect compared over a particular season. In this study, we tested whether there were significant differences between the adult life spans of three generations of the Nan tucket pine tip moth over a 2-yr period in relation to ambient temperature. We were particularly interested in seasonal temperature effects on male adults, because it is this sex which is attracted to pheromone-baited traps.

Pupal weight is often correlated with fecundity in many Lepidoptera (Engelmann 1970, Leather 1984). Furthermore, Leather and Burnand (1987) reported that reduced fecundity was associated with decreased longevity of the pine beauty moth *Panolis flammea* (Denis & Schiffermiiller) (Lepidoptera: Noctuidae), although this association is not necessarily true for other moth species. Therefore, we were also interested to see if any seasonal changes in pupal weights occurred, and if these differences were associated with seasonal changes in adult longevity. It this were so, we could infer that adult longevity may be influenced to some degree by the physiological state of the insect in the pupal stage as well as the environment during the adult stage.

Materials and Methods

Adult Longevity—Field Experiment. For each of three tip moth generations during March, June, and August 1997 and 1998, adults were reared from clipped pine shoots and collected as they emerged in cages. Up to five newly emerged moths were placed in waxed paper cans (473 ml, 8.44 cm diameter, Fonda Group, Union, NJ) with each circular end punched out and replaced by a fine mesh material (Saran screen, 12.8 X 12.8 holes/cm^2, Synthetic Industries, Cornelia, GA). Each paper can was placed in a Pherocon 1C sticky trap (Trece, Salinas, CA) to protect the moths from the elements and ant (Hymenoptera: Formicidae) predation. In 1997, all traps containing cans and moths were hung from trees in a 5-yr-old loblolly pine (Pfnus *taeda* L.) plantation in Oconee County, GA, and checked daily. In 1998, traps were similarly hung and checked daily within a 3-yr-old loblolly pine plantation in Oglethorpe County, GA.

To correlate adult life spans with field temperatures, we accumulated degree-days using maximum and minimum daily temperatures obtained from the Athens reporting station («=30 km east and northeast of each field site, respectively) of the National Oceanic and Atmospheric Administration (NOAA), National Climatic Data Center, Asheville, NC. Degree-days are a measure of accumulated heat in the environment in reference to a specified temperature range over a 24-h period. For the Nantucket pine tip moth, a lower threshold of 9.5°C and an upper threshold of 33.5°C is used. The lower threshold corresponds to the minimal temperature required for adult flight and egg development while the upper threshold represents the maximum temperature for successful egg development to occur (Haugen and Stephen 1984, Gargiullo et al. 1985). These threshold values and the daily maximum and minimum temperatures were transferred to a degree-day computation program (Degree-day Utility, University of California Statewide Integrated Pest Management [IPM] Program, Davis, CA), which uses single-sine intermediate cutoff computation methods (Seaver et al. 1990). From these daily degree-day accumulations we calculated the average daily accumulation during the life span of each moth placed in the field. Daily measures of relative humidity were also obtained from NOAA weather records for Athens, GA.

There was a concern that the interior temperature of a paper can would be elevated by being placed within a pheromone trap. To determine if this was so, measurements on temperature and humidity were taken between 1200 and 1500 hours EST inside the cans on three separate days during spring (11,23, and 30 March, *n* = 12 traps/day) and summer (16,22, and 27 June, *n* = 13 traps/day), and compared with ambient conditions just outside the trap.

Adult Longevity—Laboratory Experiments. To determine if any differences found in longevity were primarily due to temperature effects, a similar experiment was performed in the laboratory using one spring and one summer cohort of moths by placing them inside the same type of paper cans and exposing them to different constant temperatures within a temperature control unit. The moths were exposed to constant temperatures of 5, 10, 15, 20, 25, 30, 35, and 40°C. Humidity levels were kept between 40 - 60% for all temperature treatments (n = 9-41 moths/treatment). The number of moths assigned to each treatment was determined by their availability from the emergence cage.

It is not known whether tip moth adults feed. Many adult moths do not feed (Boggs 1987, Han and Gatehouse 1991), and the short life spans and activity periods of tip moths suggest that they may not either. However, if they visit nectaries or obtain energy from some other source, this would clearly affect the study because moths were prevented from obtaining any source of water or nourishment while enclosed in the cans. Two experiments were conducted in an attempt to test the importance of water or carbohydrates to adult male tip moths. In experiment 1, life span was monitored under three treatments ($n = 10$ moths/treatment) in which moths were placed individually in glass vials at 20°C with the vial opening capped with dry cotton balls (0.5 cm diameter), cotton saturated with water, and cotton saturated with a two molar sucrose solution. In experiment 2, male moths were placed individually in vials capped with dry cotton ($n = 18$ moths) or capped with-cotton saturated with a two molar sucrose solution ($n = 17$), held at 10°C, and checked daily. To prevent excess moisture from adhering to and overwhelming tip moth adults, all saturated cotton balls were gently squeezed before being placed in a vial.

Pupal Weights. Pupae were collected from each tip moth generation by clipping damaged shoots just before adult emergence. Shoots were dissected in the laboratory and pupae were collected, sexed, and weighed. In 1997, shoots from each generation were collected from plantations in Clarke, Oconee, and Morgan Counties, GA. Collections were made during February, May, July, and October. The February collection represented moths that had pupated during the previous autumn. This study was repeated from three sites in Oglethorpe county, GA, in 1999-2000. Collection dates during 1999 were from the same months as in 1997, although an additional collection from these sites was made in February 2000. This latter collection of pupae represents the same over-wintering generation as the pupae collected in October 1999. The purpose of this additional collection was to compare weights of preoverwintering pupae with those of postoverwintering pupae.

Statistical Analysis. All tests were performed using SigmaStat 2.0 (Jandel 1995). Average life spans from the field and lab were compared using Kruskal-Wallis analysis of variance (ANOVA) on ranks followed by Dunn's test for differences in ranked means. For comparison of internal and external trap conditions, a paired t-test or Wilcoxon signed rank test was used, depending on whether ANOVA assumptions were met. Pupal weights were compared using ANOVA followed by Tukey's test for multiple comparison of means or Kryskal-Wallis ANOVA on ranks and Dunn's test if ANOVA assumptions were not met. Significance levels for all tests were set at $a = 0.05$. Linear regression of average male and female life spans on average daily degree-day accumulation was performed using Sigmaplot4.0 (SPSS 1997).

Results

Adult Longevity—Field Experiment. During 1997 and 1998, male moths lived significantly longer during the first generation than the second and third generations (1997, $H = 33.08$; df = 2; $P < 0.001$; 1998, $H = 48.40$; df = 2; $P < 0.001$) (Fig. 1). Adult females from the first generation lived significantly longer than those from the second generation in 1997 ($H = 19.47$; df = 2; $P < 0.001$), while in 1998 females from the first generation lived significantly longer than those from the second and third generations ($H = 33.39$; df = 2; $P < 0.001$) (Fig. 1). Average daily degree-day accumulations were inversely related to adult life span for males and females (Fig. 2). Linear models explained 90% ($P < 0.001$) and 89% ($P < 0.001$) of the variation in this relationship for males and females, respectively. In 1997, first, second, and third generation males were exposed to an average (±SD) of 5.8 (±0.5), 15.6 (±0.5), and 15.6 (±2.6) DD per day, respectively. Females from the first, second, and third generations of 1997 were exposed to an average of 6.0 (±0.3), 16.7 (±0.8), and 15.0 (±1.0) DD per day, respectively. Similarly, males in 1998 were exposed to 3.5 (±1.5), 15.1 (±1.9), and 16.9 (±1.7) DD per day for each successive generation, whereas females during this year were exposed to 5.4 (±1.8), 15.9 (±1.8), and 16.7 (±1.3) DD per day, respectively.

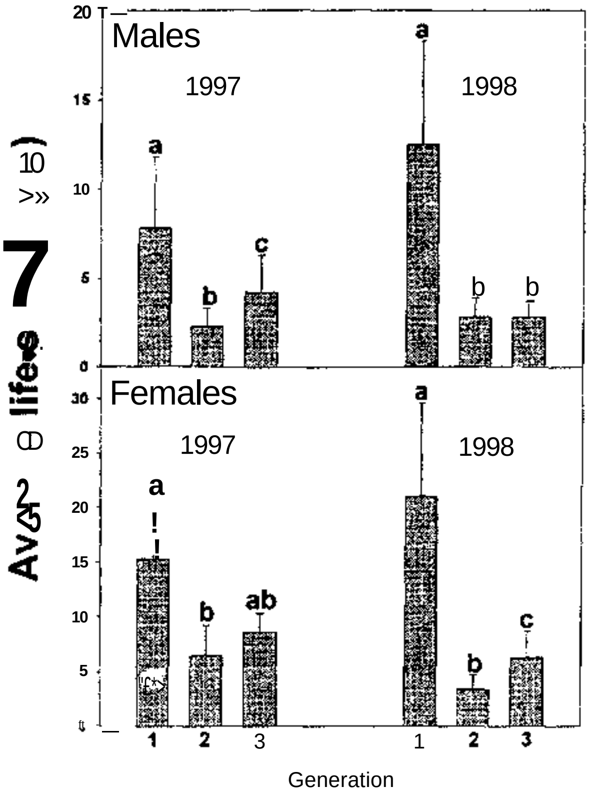

Fig. 1. Average (±SD) life span of each generation of adult Nantucket pine tip moth males and females in a loblolly pine plantation near Athens, GA, during 1997 and 1998. Within each year, means followed by the same letter are not significantly different at $a = 0.05$ (Dunn's method).

Average (±SD) daily temperature and humidity during the 1997 field experiment was 15.1°C (±2.8) and 57.0% (±16.7), respectively, for first generation moths (18Marchto 11 April),26.1°C (±1.5) and74.8% (±5.7) for second generation moths (19 June to 6 July), and 25°C (±2.7) and 64.5% (±7.8) for the third generation moths (14 August to 7 September). Similarly, the average daily temperature and humidity during the 1998 field experiment was 13.1°C (±4.7) and 69.5% (±17.0) for the first generation (28 February to

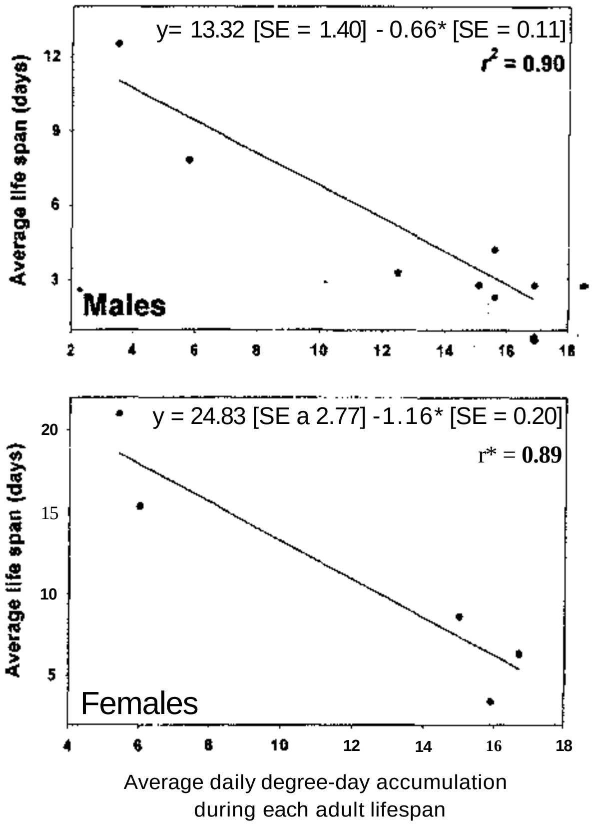

Fig. 2. Relationship between adult Nantucket pine tip moth male and female average life span and the average daily degree-day accumulation during each generation and each year of the study.

4 May), 25°C (±3.0) and 66.2% (±9.2) for the second generation (4 June to 16 June), and 26.6°C (±1.7) and 64.0% (±9.2) for the third generation (23 July to 6 August).

Internal trap temperatures were 1.0 and 0.5°C higher, respectively, than ambient during spring (t = -3.54; df = 11; P = 0.005) and summer (t = -3.18; df = 12; P = 0.008), while internal humidity was 2.8% lower than ambient during spring (W = -52.0; df = 11; P = 0.042) (Table 1). However, these differences were so minor that they are not thought to have had any influence on adult longevity.

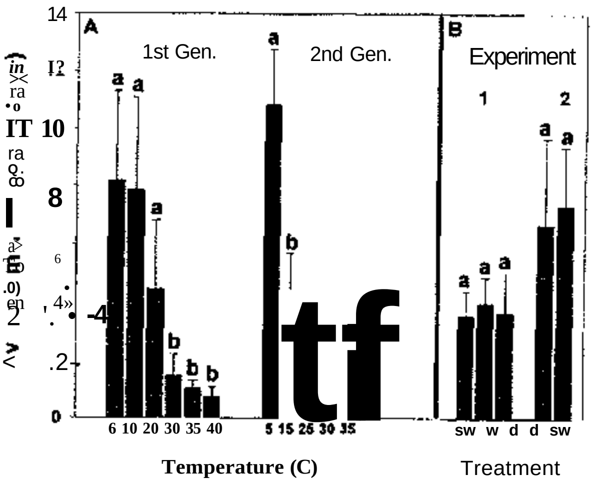

Fig. 3. (A) Average (±SD) life span of adult Nantucket pine tip moth males under different constant temperatures using moths from the first and second generations. (B) Two experiments comparing male moth life span under different treatments (sw = sugar water, w = water only, d = dry) and constant temperatures (experiment 1-20°C, experiment 2-10°C).

Adult Longevity—Laboratory Experiments. For first generation males, the average life span within the first three treatments were all significantly different from the latter three (H = 106.99; df = 5; P < 0.001) (Fig. 3A). For second-generation males, only the average life span from the first treatment was significantly different from the latter four treatments (H = 47.93; df = 4; P < 0.001) (Fig. 3A). No significant differences in adult male life span were found for any of the treatments involving dry cotton, cotton saturated with water, or cotton saturated with a two molar sucrose solution (experiment 1, H = 1.20; df = 2; P = 0.549; experiment 2, X = 344.5; P = 0.210) (Fig. 3B).

Pupal Weights. There were no significant differences among male pupal weights at any of the collection sites from 1997 (Oconee County, F = 1.32; df = 2, 56; P = 0.275; Clarke County, F = 1.70; df = 3, 79; P = 0.174; Morgan County, F = 1.91; df = 3, 37; P = 0.147) (Table 2). For females at these same sites, pupal weights tended to be significantly higher from the May, July, and October 1997 collections compared with the February 1997 collection (Oconee County, F = 14.16; df = 2, 63; P < 0.001; Clarke County, F = 2.65; df = 3, 88; P = 0.054; Morgan County, F = 3.48; df = 3,35; P = 0.027) (Table 2). For male weights from the 1999 collections, there were a few significant differences among generations but no consistent pattern in weight changes throughout the year (Arnoldsville, F = 4.69; df = 3,100; P = 0.004; Maxeys, F = 0.24; df = 3,109; P = 0.870; Lexington, F = 5.32; df = 4,148; P < 0.001) (Table 3). Furthermore, there were no significant changes in weights of overwintering male pupae at any site from October 1999 to February 2000 (Table 3). For female weights from the 1999 collections, only one collection at one site from May 1999 was statistically different from any of the others, and there were no significant changes in weight of overwintering female pupae at any site from October 1999 to February 2000 (Arnoldsville, F = 1.10; df = 3, 111; P = 0.352;

Table 1. Comparison of ambient temperature (°C) and relative humidity with the interior of traps used in the study

Season / Location	Avg temp[a]	Avg humidity
Spring/Ambient	14.8a	46.4%c
Spring/Interior	15.8b	43.6%d
Summer/Ambient	31.2a	52.2%c
Summer/ Interior	31.7b	52.7%c

[a] Within each season and variable measure, means followed by the same letter are not significantly different (paired t-test or Wilcoxon signed rank test, α = 0.05).

Table 2. Average pupal weight in mg(±SD) of each generation of males and females collected in Clarke, Oconee, and Morgan Counties, Georgia, in 1997

Site/Sex	Feb 1997	May 1997	July 1997	**Oct 1997**
Oconee County males"	5.76 (±0.98) a (**n** = 29)	5.78 (±0.75) a **(ii = 9)**	6.19 (±0.87) a (n = **18)**	No data collected
Clarke County males	5.45 (±1.43)a **(ii = 11)**	6.33 (±0.99) a (**n** = 23)	6.00 (±0.26) a (n = 3)	6.15 (±1.06)a **(ii = 42)**
Morgiui County males	5.12 **(±0.58)a** **(ii = 5)**	6.30 (±1.10)a **(ii = 13)**	5.94 (±0.96) a (n = 8)	6.14 (±0.90) a (» = 11)
Oconee County • females	**7.47 (±1.42)a** (» = 34)	9.47 (±1.86)b (n = 12)	9.72 (±1.74)b (n = 17)	No data collected
Clarke County females	7.94 (±1.26) a (II = **11)**	9.01 (±1.97)ab (**n** = 24)	10.01 (±1.91)b (» = 8)	9.22 (±L£5)ab (*n* = 45)
Morgan County females	7.46 (±1.10) a (» = 5)	9.72 (±1.73)b (n = 18)	9.57 (±1.50)ab **(ii = 3)**	8.52 (±1.17)ab (**n** = 9)

" Within each site, means followed by the same letter are not significantly different (Tukey's test, ***a*** = 0.05)

Maxeys, H = 6.20, df = 3, P = 0.102; Lexington, F = 5.11; df = 4, 152; P < 0.001) (Table 3).

Discussion

During both years of the field study, it was demonstrated that Nantucket pine tip moth adults do experience decreased longevity during the second and third generations when temperatures are significantly warmer. Among the environmental or physiological factors that may influence adult longevity, temperature appears to be one of the more important factors. In the laboratory experiments, humidity was kept between 40 and 60% in the temperature control units, and moths kept in vials capped with saturated cotton did not live longer than those in vials capped with dry cotton under the same constant temperatures. Although humidity was not measured inside the vials, it was likely higher in those that were capped with saturated cotton because tiny droplets of condensation were observed in these vials. Furthermore, average humidity levels during the 1997 field experiment were lower in spring than in summer, while in 1998, they were almost the same between seasons. Since these variations were not correlated with the seasonal change in adult longevity, it appears that humidity is not as important as temperature in affecting adult life span. Although the environment of the paper cans was a concern, the small differences in temperature and humidity within the can and the ambient conditions did not appear to have any effect on life span.

Butler and Foster (1979) showed that adults of the pink boll worm, *Pectinophora gossypiella* (Saunders) (Lepidoptera: Gelechiidae), held at constant temperatures lived longer than at comparable, fluctuating temperatures. Pilon (1966) also demonstrated shorter life span under fluctuating than constant temperatures for both sexes of the Swain jack pine sawfly. For the Nantucket pine tip moth, life spans in the field experiment closely matched those in the laboratory experiment under similar average temperatures (Figs. 1 and 3). The constant temperatures used in the lab experiments did not appear to affect this species.

Other factors that may have influenced adult longevity include the moth's inability to fly very far and expend metabolic energy (Boggs 1987), an inability to mate, and an inability to feed or drink. Nantucket pine tip moths mate infrequently and produce few viable eggs when caged in the laboratory or confined to small spaces (Cresswell et al. 1971, Richmond and Thomas 1977). Partridge and Farquhar (1981) demonstrated that sexual activity reduces the life span of male fruit flies (Diptera: Tephritidae) while Moscardi et al. (1981) showed that unmated females of the velvet-

Table 3. Average pupal weight in mg (±SD) of each generation of males and females collected at three sites in Oglethorpe County, Georgia, in 1999-2000

Site/Sex	Feb 1999	May 1999	July 1999	Oct 1999"	Feb 2000^
Arnoldsville males"	6.17 (±0.99)ab (» = 28)	No data collected	. 5.79(±0.92)b (n=9)	6.81 (±0.71)ac (n = 24)	6.72 (±0.98)ac **(ii = 43)**
Maxeys males	6.42 (±0.82) a **(ii = 42)**	6.27 (±0.97) a **(ii = 19)**	No data collected	6.25 (±0.89) a **(ii = 28)**	6.27 (±1.23)a **(ii = 24)**
Lexington males	5.86 (±0.87) a (» = 40)	6.a5 (±0.94) ab (n = 40)	5.87 (±1.02) a **(ii = 19)**	6.89 (±1.12)b (» = 25)	6.20 (±0.87)ab **(ii = 29)**
Arnoldsville females	8.00(±1.51)a (n = 35)	No data collected	8.68 (±1.16)a (» = 4)	8.66 (±1.52)a **(ii = .30)**	8.19 (±1.62)a **(ii = 46)**
Miixeys females	8.00 (±1.78) a (II = 39)	9.06 (±1.21) a (n = 14)	No data collected	8.69 (±1.56)a **(ii = 20)**	8.78 (±2.06) a (» = 27)
Lexington females	7.66 (±1.37) a **(ii = 40)**	9.16(±1.79)b **(ii = 40)**	7.78 (±2.10)ab (n = 12)	8.46 (±1.39) ab **(ii = 34)**	8.23 (±1.40)ab (" = **31)**

" Within each site, means followed by the same letter are not significantly different (Tukey's test or Dunn's test^c, *a* = 0.05)
" Note: These two columns represent pupae from the same generation.

bean caterpillar lived significantly longer than mated females at a given temperature. Although male and female tip moths were mixed together in half of the paper cans placed in the field, there were no differences in the life span of either sex compared with those that were placed in same-sex cans (data not shown). The extent to which adult tip moths feed or drink, if at all, is unknown. In their studies of the pine beauty moth, Leather and Burnand (1987) reported that unfed female adults had a shorter life span. Leahy and Andow (1994) showed that diets'with sugars significantly increased oviposition period, fecundity, and adult longevity in the European corn borer, *Ostrinia nubilalis* (Hiibner) (Lepidoptera: Pyralidae). Howell (1981) observed a 6- to 12-d increase in adult longevity of the codling moth when provided water, carbohydrate, or a carbohydrate-protein solution, but no increase in mating, oviposition, or egg viability. Kira et al. (1969) reported that water was the most important feeding requirement for adults of the European corn borer. Our lab experiments involving sugar solution (Fig. 3) were inconclusive. Although there were no differences between treatments, we can only conclude that adults do not feed or that they were not stimulated to do so under these specific conditions. It is clear, however, that addition of food and water did not affect the life span of adult moths in captivity. There are a number of species of moths that do not feed as adults (Boggs 1987, Han and Gatehouse 1991). Indeed, in many species of Lepidoptera, the maximal number of eggs an individual can lay is proportional to the amount of stored nutrient reserves acquired during larval feeding (Engelmann 1970). In other species, carbohydrates obtained during adult feeding are either used immediately in oogenesis or stored as glycogen in the fat body and used after hydrolysis. Glycogen seems to be involved in the maintenance of body weight and oocyte production (Kozhantshikov 1938, Chapman 1982).

Pupal weights of both males and females showed no important differences overall among the three generations and were very similar across all sites. There does not appear to be a relationship between these weights and life span of the adults. There also is no significant loss of pupal weight during the overwintering period. If a substantial weight loss occurred in pupae during the overwintering period, and pupal weight was a direct predictor of adult longevity as it is for fecundity, then adults emerging in spring would have a shorter life span under the same temperature compared with a summer emerging cohort. The laboratory experiments (Fig. 3) appear to support this possibility, since the second generation of moths used lived longer overall than the first generation moths over the same range of temperatures. However, the experiment was not originally designed to show this and these differences were not tested statistically. In one set of pupal weights (Table 3), overwintering females showed statistically lower weights than those in subsequent generations. Whether these weight differences are biologically meaningful is unknown, although average fall/winter temperatures (October through February) in 1996/1997 were colder than in 1998/1999 (1996/1997, 9.9°C; 1998/1999, 11.9°C).

There is a pronounced difference in adult longevity between spring and summer. This helps to explain why summer trap catches of the Nantucket pine tip moth often drop precipitously from spring to summer despite constant or increasing populations. This should be taken into account when using traps to monitor moths and making population estimates based on trap catch.

-Ael*n<twledgments

We thank K. Rhodes and B. Dorough for assisting with this study. Thanks also to C. Fettig and J. Nowak, who reviewed an earlier version of the manuscript. We are indebted to J. Cook and the former Champion International Corporation for permission to conduct research on their lands. This work was supported by funds provided by the Pine Tip Moth Research Consortium.

References Cited

Asaro, C, and C. W. Berisford. 2001. Predicting infestation levels of the Nantucket pine tip moth (Lepidoptera: Tortricidae) using pheromone traps. Environ. Entomol. 30: 776-784.

Bari, M. A., and W. H. Lange. 1980. Influence of temperature on the development, fecundity, and longevity of the artichoke plume moth. Environ. Entomol. 9: 673-676.

Berisford, C. W. 1974. Comparisons of emergence periods and generations of the pine tip moths, *Rhyacionia frwtrana* and *R. rigidana.* Ann. Entomol. Soc. Am. 67: 666-668.

Berisford, C. W. 1988. The Nantucket pine tip moth, pp. 141-161. *In* A. A. Berryman [ed.], Dynamics of forest insect populations. Plenum Publishing, London.

Berisford, C. W., C. G. Canalos, J. F. Godbee, Jr., and H. O. Yates, III. 1992. Occurrence and seasonal activity of pine tip moths in Georgia. Ga. For. Comm. Res. Div. Ga. For. Res. Pap. 87.

Boggs, C. L. 1987. Ecology of nectar and pollen feeding Lepidoptera, pp. 369-392. *In* F. Slansky and J. G. Rodriguez [eds.J, Nutritional ecology of insects, mites, spiders, and related invertebrates. John Wiley and Sons, New York.

Butler, G.D., and R. N.Foster. 1979. Longevity of adult pink bollworms at constant and fluctuating temperatures. Ann. Entomol. Soc. Am. 72: 267-268.

Byers, J. A., and J. Löfqvist. 1989. Flight initiation and survival in the bark beetle *Ips typographus* (Coleoptera: Scolytidae) during the spring dispersal. Holarct. Ecol. 12: 432-440.

Byers, J. A., O. Anderbrant and J. Löfqvist. 1989. Effective attraction radius: a method for comparing species attractants and determining densities of flying insects. J. Chem. Ecol. 15: 749-765.

Canalos, C. G., and C. W. Berisford. 1981. Seasonal activity of two sympatric *Rhyacionia* species as determined by pheromone traps. J. Ga. Entomol. Soc. 16: 219-222.

Comeau, A., R. T. Cardé, and W. L. Roelofs. 1976. Relationship of ambient temperatures to diel periodicities of sex attraction in six species of Lepidoptera. Can. Entomol. 108: 415-418.

Chapman, R. F. 1982. The insects: structure and function, 3rd ed. Harvard University Press, Cambridge.

Cresswell, M. J., E. E. Sturgeon, and R. D. Eikenbary. 1971. Laboratory rearing of the Nantucket pine tip moth, *Rhyacionia frustrana,* on artificial diets. Ann. Entomol. Soc. Am. 64: 9-63.

Engelmann, F. 1970. The physiology of insect reproduction. Pergamon, Oxford.

Fettig, C. J., and C. W. Berisford. 1999. Nantucket pine tip moth phenology in eastern North Carolina and Virginia, implications for effective timing of insecticide applications. South. J. Appl. For 23: 30 -.38.

fettig, C.J., M.J. Dalysky, and C. W. Berisford. 2000. Nantucket pine tip moth phenology and timing of insecticide spray applications in seven southeastern states". U.S. Dep. Agric For. Serv.'Res. Pap. SRS-18.

Gargiullo, P. M, C. W. Berisford, and J. F. Godbee. 1985. Prediction of optimal timing for chemical control of the Nantucket pine tip moth, *Rhyacionia frustrana* (Cornstock) (Lepidoptera: Tortricidae) in the southeastern coastal plain. J. Econ. Entomol. 78: 148-154.

Han, E., and A. G. Gatehouse. 1991. The effect of adult feeding on female pre-calling period and ovarian development in a migratory moth, the oriental armyworm *Mythimna sejiarata* (Lepidoptera: Noctuidae). Bull. Entomol. Res. 81: 395-400.

Haugen,D. A., and F.M.Stephen. 1984. Development rates of the Nantucket pine tip moth, *Rhyacionia frustrana* (Comstock) (Lepidoptera: Tortricidae) life stages in relation to temperature. Environ. Entomol. 13: 56-60.

Howell,J. F. 1981. Codling moth: The effect of adult diet on longevity, fecundity, fertility, and mating. J. Econ. Entomol. 74: 13-18.

Jandel Corporation. 1995. Sigmastat statistical software user's manual, version 2.0. San Rafael, CA.

JSnsson, P., and O. Anderbrant. 1993. Weather factors influencing catch of *Neodiprion sertifer* (Hymenoptera: Diprionidae) in pheromone traps. Environ. Entomol. 22: 445-452.

Kira, M. T., W. D. Guthrie, and J. L. Huggans. 1969. Effect of drinking water on production of eggs by the European corn borer. J. Econ. Entomol. 62: 1366-1368.

Kozhantshikov, I. W. 1938. Carbohydrate and fat metabolism in adult Lepidoptera. Bull. Entomol. Res 29:103-114.

Leahy, T. C, and D. A. Andow. 1994. Egg weight, fecundity, and longevity are increased by adult feeding in *Ostrinia nubilalis* (Lepidoptera: Pyralidae). Ann. Entomol. Soc. Am. 87: 342-349.

Leather, S. R. 1984. Factors affecting pupal survival and eclosion in the pine beauty moth, *Panolis fiammea* (D & S). Oecologia63: 75-79.

Leather, S. R., and A. C. Burnand. 1987. Factors affecting life-history parameters of the pine beauty moth, *Panolis fl.am.mea* (D&S): the hidden costs of reproduction. Funct. Ecol. 1: 331-338.

Mason, L.J., and T. P. Mack. 1984. Influence of temperature on oviposition and adult female longevity for the soybean looper, *Pseudoplusia inckulens* (Walker) (Lepidoptera: Noctuidae). Environ. Entomol. 13: 379-383.

Moscardi, F., C. S. Barfield, and G. E. Allen. 1981. Effects of temperature on adult velvetbean caterpillar oviposition, egg hatch, and longevity. Ann. Entomol. Soc. Am. 74: 167-171.

Nakamura, K., and K. Kawasaki. 1984. Male catches of *Spodoptera lifura* (F.) in pheromone traps under fluctuating wind velocity: validity of the active space model. Appl. Entomol. Zool. 19: 192-201.

Partridge, L., and M. Farquhar. 1981. Sexual activity reduces life span of male fruitflies. Nature (Lond.) 294: 580-.582.

Pilon,J. G. 1966. Influence of temperature and relative humidity on the life-span of adults of the Swain jack pine sawfly, *Neodiprion swainei* Middleton, (Hymenoptera. Diprionidae). Can. Entomol. 98: 789-794.

Pitcairn, M. J., F. G. Zalom, and W. J. Bentley. 1990. Weather factors influencing capture of *Cydia pomonella* (Lepidoptera. Tortricidae) in pheromone traps during the overwintering flight in California. Environ. Entomol. 19: 1253-1258.

Richmond, J. A., and H.A.Thomas. 1977. Induced mating of the Nantucket pine tip moth, *Rhyacionia. frustrana,* in the laboratory. J. Ga. Entomol. Soc. 12: 312-317.

Seaver, D., J. Strand, and A. J. Strawn. 1990. Degree-day utility user's guide, version 2. University of California, Davis.

SPSS Incorporated. 1997. Sigmaplot User's Manual, Version 4.0, Chicago, IL.

Teulon, D.A.J., and D. R. Penman. 1991. Effects of temperature and diet on oviposition rate and development time of the New Zealand flower thrips, *Thrips ohscuratus.* Entomol. Exp. Appl. 60: 143-155.

WebbJ. W., and C. W. Berisford. 1978. Temperature modification of flight and response to pheromones in *Rhyacionia frustrana.* Environ. Entomol. 7: 278-280.

Received for publication 22 November 2000; accepted 17 July 2001.