Impact of Photoperiod on the Sexual Behavior of the Black Cutworm Moth (Lepidoptera: Noctuidae)

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ABSTRACT   We tested the hypothesis that changes in photoperiod alone are responsible for the delay in the onset of sexual maturity that has been previously observed in natural populations of the migratory black cutworm, *Agrotis ipsilon* (Hufnagel), moth. We hypothesized that under short days, which occur at the onset of the spring and fall migrations, the first age at which males and females engage in sexual communication would be later than under long days typical of nonmigratory periods. Individuals were kept at 25°C from egg to adult under three photoregimes that they encounter in nature at different latitudes: 12:12 (L:D) h (late March and late September), 14:10 (L:D) h, and 16:8 (L:D) h. As predicted, the mean age at which females first called (i. e., released pheromone) was earlier under long-day than under short-day photoregimes, but this trend was not significant. The percentage of females that called over a 6-d-period was similar among photoregimes but it varied with age. There was no interaction between photoperiod and age on the percentage of females calling. Pheromone production, measured as the quantity of Z7–12:Ac in pheromone gland extracts, was lower under long-day than under short-day photoregimes. On average, 1-d-old females produced less pheromone than older females. Photoperiod and age showed a significant interaction in their effect on the quantity of Z7–12:Ac, but not in the direction predicted by our hypothesis. Males reared under short days showed higher percentages of response than did males reared under long days. Age had a significant effect on male response but it was independent from the effect of photoperiod. We conclude that although photoperiod length can influence calling, pheromone production, and male response, it has little effect on the age at which *A. ipsilon* reach sexual maturity. Changes in photoperiod alone cannot explain the delayed maturity observed in the field. Other factors, alone or in combination with photoperiod, may be necessary to induce the reproductive diapause that *A. ipsilon* undergoes in its fall migration.

KEY WORDS black cutworm moth, sex pheromone, migration, reproductive diapause, calling, periodicity

IN MIGRATORY INSECT species, individuals that engage in migratory behavior usually undergo changes in their morphological, physiological, and behavioral traits (the so-called "migration syndrome") that facilitate long-duration flight and successful colonization of new habitats (Dingle 1985, Drake et al. 1995). An example of morphological changes related to migration is the existence of two wing forms, a wingless (aphids) or brachypterous (planthoppers, water striders, grasshoppers) form unable to fly, and a winged or macropterous form that can (Dingle 1985, Zera and Denno 1997). Less apparent differences between migratory and nonmigratory forms occur at the physiological and behavioral levels. In several insect species, migration is preceded by a prereproductive period that extends until the migration is finished (Gatehouse and Zhang 1995, Gatehouse 1997). This "oogenesis-flight syndrome" (Johnson 1969) is not observed in the nonmigratory individuals of the population and is thought to be an adaptation to optimize migration and reproduction, which are metabolically demanding and use similar energy reserves (Rankin and Burchsted 1992, Dudley 1995).

Some of the cues used by insects to predict changes in environmental quality in relation to migration include overcrowding and changes in host quality, but temperature and photoperiod are probably the most universal cues (Tauber et al. 1986, Danks 1987). Several studies have reported the effect of photoperiod or temperature on the onset of reproduction and its relation with migration in insects (Herman 1973, Dingle 1978, McNeil et al. 1995, Taylor et al. 1995). The black cutworm, *Agrotis ipsilon* (Hufnagel), migrates in most of its range and is one of the few species for which complete two-way migration has been demonstrated experimentally (Showers et al. 1993, Showers 1997). In North America, a colonizing generation of *A. ipsilon* migrates northward in the spring (Kaster and Showers 1982, Showers et al. 1989, Hendrix and Showers 1992) and a later generation migrates southward in the fall (Showers et al. 1993). It has been suggested that *A. ipsilon* enters reproductive diapause, or delayed maturity, before its annual southward migration (Kaster

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and Showers 1982) because late in the season more males are attracted to light traps than to pheromone traps (Willson et al. 1981, Kaster and Showers 1982, Levine et al. 1982) and most females remain unmated (Kaster and Showers 1982, Clement et al. 1985).

These observations prompted us to investigate the effect of photoperiod on the reproductive maturity of *A. ipsilon.* We reared individuals from egg to adult under three photoregimes experienced by this species under natural conditions at different latitudes and times of the year. We observed the potential interaction between photoperiod and age on the quantity of pheromone produced by the females, calling behavior by females, and percent response by males to a pheromone source. We hypothesized that if photoperiod is the main cue influencing the length of the prereproductive period in *A. ipsilon,* adults will mature at an earlier age under long-day than under short-day conditions.

Materials and Methods

Insects. Colony origin, maintenance, and rearing conditions followed procedures of Gemeno and Haynes (1998). Ovipositing females were maintained at room temperature under a photoregime of 14:10 (L:D) h. Larvae were reared in one of three photoregimes at 25°C. The photoregimes cover most of the natural day-lengths that *A. ipsilon* experiences in North America, between early-spring and early-fall, including 12:12, 14:10, and 16:8 (L:D) h. In all three photoregimes the scotophase began at the same time of the day. Larvae were reared in individual cells and were covered with a translucent and breathable construction material (Porex, Fairburn, GA). Female pupae were placed individually in 475-ml paper containers covered with nylon screen. Male pupae were placed in 3.78-liter paper containers covered with nylon screen at a density of ≈40 individuals per container. Females were maintained in the same three chambers where the larvae developed. Males were maintained in two different chambers, one in continuous light and another in continuous dark, unexposed to the sex pheromone released by the females. Transfer of males from the light chamber to the dark chamber at the appropriate times served to maintain the same photoperiodic conditions under which they developed. Adults were given access to 10% sucrose-water solution and were considered to be 1 d old starting the day of emergence.

Calling Behavior. Observations of calling behavior followed procedures of Gemeno and Haynes (2000). Females were transferred individually to 475-ml clear-plastic containers during the first 2 h of the photophase preceding the scotophase of observation. Observations were aided with a flashlight covered with a red-photographic filter, which did not disturb the behavior of the females.

Females were observed throughout the scotophase at 30-min intervals starting the day of emergence and for a period of 6 d ($n = 12$/photoregime). Ages were pooled to calculate the duration, onset and mean times of calling for each photoperiod. The time between these calling parameters and the lights-on, lights off, mid-photophase and mid-scotophase were compared among photoregimes with analysis of variance (ANOVA) of log-transformed data. To determine if photoregime and calling age influenced the percentage of females calling we used a logistic regression.

To calculate the age at which females called for the first time we used the previous sample of females plus a group of females that was observed only until the day they called for the first time and then were discarded ($n = 22$–23). To test if photoperiod had an effect on first age of calling we performed a linear contrast of the photoperiods using log-transformed data.

Sex Pheromone Extraction and Analysis. The ovipositors and associated pheromone glands of 1- to 6-d-old females were excised during the second half of the scotophase of each photoregime ($n = 7$–9 females/age/photoregime). Nontegumentary tissues were removed carefully using fine forceps and the glands were placed individually in 10 μl of methylene chloride containing 1 ng of internal standard, (*E,Z*)-4,7-tridecadienyl acetate (*E,Z*-4,7–13:Ac). Gland extracts were kept for 1–2 h at room temperature and then frozen at −80°C before analysis with a gas chromatograph and a mass selective detector (MSD) following the procedures of Gemeno and Haynes (2000). We conducted selected ion monitoring focusing on the ions characteristic of the major pheromone component, (*Z*)-7-dodecenyl acetate (*Z*7–12:Ac), and of *E,Z*-4,7–13:Ac (*m/z*, 166 and 178, respectively). Photoregime and age effects on the quantity of *Z*7–12:Ac were calculated with ANOVA on log-transformed data.

Male Response. The response of 1- to 6-d-old males to synthetic pheromone blend (*Z*7–12:Ac, [*Z*]-9-tetradecenyl acetate [*Z*9–14:Ac], and (*Z*)-11-hexadecenyl acetate [*Z*11–16:Ac], 3:1:6 μg in 50 μl of n-hexane) was observed during the last 4 h of the scotophase of each photoregime in a wind tunnel. Wind tunnel, light conditions, wind speed, and insect handling were as previously reported (Gemeno and Haynes 1998). Males were placed in the downwind end of the tunnel on a platform 25 cm above the floor. The pheromone blend, which was loaded on a rubber septum at least 60 min before the test, was placed 1.5 m upwind from the male in the center of the tunnel, 26 cm above the floor. After allowing flight of one male from each treatment (6 ages × 3 photoregimes = 18 treatments) a new rubber septum was used. Between 11 and 20 males were tested for each age and photoregime combination. After release, male behavior was observed for 2 min. We recorded oriented upwind flight (a zigzagging flight in the pheromone plume that is characteristic of male moths responding to a pheromone source) and pheromone source contact. Each male was used only once. To determine the effect of photoperiod and age on the response of the males we used a cumulative logits model (Agresti 1990).
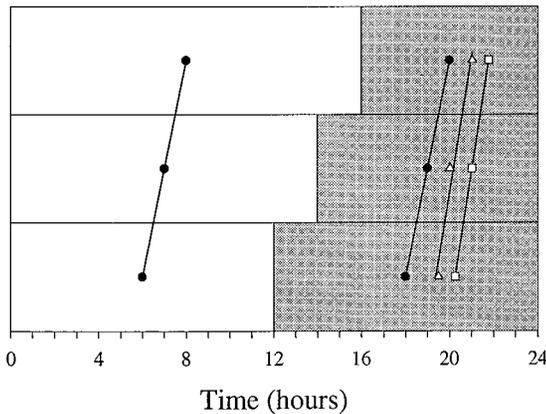
Fig. 1. Onset (triangles) and mean (squares) times of calling of *Agrotis ipsilon* virgin females reared under three photoregime conditions (white bar = photophase, gray bar = scotophase; 12:12, 14:10, and 16:8 [L: D] h) in relation to lights-on, lights-off, mid-photophase (black dots on white area), and mid-scotophase (black dots on gray area).

Results

Calling Behavior. Calling was observed mainly during the second half of the scotophase and near the middle of this half in all three photoregimes (Fig. 1). The period of calling relative to the onset and end of the scotophase varied across photoregimes and did not maintain a constant phase relationship with either lights-off or lights-on. As the length of the scotophase increased the onset time of calling occurred later with respect to the onset of the scotophase (Fig. 1; $F = 98.81$; df = 2, 162; $P < 0.01$) and earlier with respect to the onset of the photophase, and in this case there was a significant interaction between age and photoregime (Fig. 1). The same trend was observed with the mean time of calling for lights-off ($F = 226.18$; df = 2, 162; $P < 0.01$) and lights-on. The period of calling did not maintain a constant phase relationship with either the mid-photophase or mid-scotophase as shown by longer time intervals between the onset of calling and mid-scotophase or mid-photophase ($F = 5.4$; df = 2, 162; $P < 0.01$, and $F = 5.53$; df = 2, 162; $P < 0.01$, respectively) and between the mean time of calling and mid-scotophase or mid-photophase ($F = 9.83$; df = 2, 162; $P < 0.001$, and $F = 9.59$; df = 2, 162; $P < 0.01$) as the length of the night increased. Calling

Table 1. Percentages of 1- to 6-d-old virgin females of *Agrotis ipsilon* maintained under three photoregimes that exhibited calling behavior ($n = 11–12$)

Age	Photoregime			Totals by age
	12:12	14:10	16:8	
1	58.33	50	66.6	58.33
2	72.72	66.66	91.66	77.14
3	100	83.33	91.66	91.43
4	90.91	91.66	83.33	88.57
5	90.91	75	91.66	85.71
6	100	83.33	83.33	88.57
Totals by photoregime	85	75	84.72	

duration was similar across photoperiods (min ± SE: 121.61 ± 8.28, 150 ± 8.79, 119 ± 8.44, 12:12, 14:10, 16:8 (L:D) h, respectively; $F = 2.99$; df = 2, 162; $P = 0.05$).

Under all photoregimes, almost 50% of the females had called for the first time by age 1, and >75% by age 2. Almost all the females had called by age 3, except for three females that did not call until 4 d old and one female that did not call until 5 d old (these females made 5.88% of the total sample). The mean ± SE first ages of calling were 1.83 ± 0.2, 1.74 ± 0.19, and 1.68 ± 0.21 d from adult emergence for 12:12, 14:10, and 16:8 (L:D) h, respectively. Although there was a trend for progressively earlier first ages of calling from short-day to long-day photoregimes, it was not significant ($F = 0.3$; df = 1, 65; $P = 0.58$).

The percentage of females calling was not affected by photoperiod ($\chi^2 = 0.65$, df = 2, $P = 0.72$) (Table 1). There was no interaction between age and photoperiod for the percentage of females calling. Percentages of calling per night ranged from 50 to 100%. Age affected the percentage of females calling ($\chi^2 = 4.52$, df = 1, $P = 0.03$), reflecting the higher percentages of calling of the middle age groups. Sample size ranged from 11 to 12 individuals because some females died before the observations ended.

Sex Pheromone. The interaction between age and photoregime was significant ($F = 1.91$; df = 10, 123; $P = 0.04$), but with no trend in the direction of our hypothesis. Young females reared under the long-day photoregimes did not have more pheromone than similar age females reared under the short-day photoregimes (Table 2). Overall, females reared under long-day photoregimes contained less pheromone in their glands than females reared under short-day con-

Table 2. Quantity of Z7-12:Ac in pheromone gland extracts of 1- to 6-d-old *Agrotis ipsilon* virgin females reared under three photoregimes ($n = 7–9$)

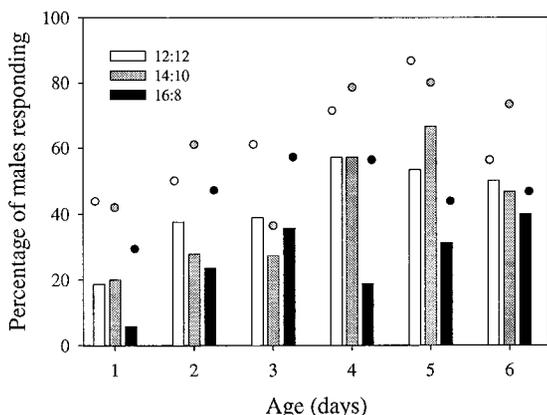| Age	Photoregime			Means by age
	12:12	14:10	16:8	
1	41.62 ± 11.71	51.43 ± 8.71	44.33 ± 8.12	45.97 ± 5.28
2	86.08 ± 12.95	39.04 ± 10.05	62.10 ± 7.95	62.42 ± 7.24
3	68.12 ± 10.30	73.39 ± 6.32	56.80 ± 12.82	66.1 ± 5.8
4	77.62 ± 9.86	42.12 ± 11.31	60.75 ± 10.43	60.16 ± 6.56
5	80.85 ± 9.01	78.67 ± 13.50	59.12 ± 10.45	73.14 ± 6.62
6	61.93 ± 9.25	61.00 ± 3.63	32.31 ± 9.02	52.15 ± 5.18
Means by photoregime	69.55 ± 4.6	57.61 ± 4.25	52.22 ± 4.18	

Fig. 2. Percentages of oriented upwind flight (dots) and contact (bars) with a synthetic pheromone blend source (Z7–12: Ac, Z9–14: Ac, and Z11–16: Ac, 3:1: 6 μg) in a wind tunnel bioassay by 1- to 6-d-old *Agrotis ipsilon* males reared under three photoregime conditions ($n = 11$–20). White: 12:12 (L: D) h, gray: 14:10 (L: D) h, black: 16:8 (L: D) h.

ditions and the quantity of pheromone was lower for 1- and 6-d-old females than in females of other ages.

Male Response. There was no significant interaction between age and photoperiod on the response of the males. Percentage of oriented upwind flight reached or surpassed 80% under photoregimes of 12:12 (L:D) and 14:10 (L:D) h, but it did not reach 60% under 16:8 (L:D) h. Male response was significantly affected by the photoregime (Fig. 2; $\chi^2 = 8.54$, df = 2, $P = 0.01$). Total percentages of males orienting per photoregime were 61.7, 63.4, and 38.3% for 12:12, 14:10, and 16:8 (L:D) h, respectively. Age also had a significant effect on the percentage of males responding ($\chi^2 = 18.18$, df = 5, $P < 0.01$). Total percentages of upwind flight per age were 40.4, 52.9, 53.5, 68.2, 69.6, and 62.2% for 1- to 6-d-old males, respectively.

Discussion

Agrotis ipsilon maintained from egg to adult under three photoperiod conditions showed differences in several aspects of their reproductive behavior, but only the advance in the first age of calling under long-days (or delayed first age of calling under short-days), although not significant, agreed with our hypothesis. Similar results were obtained in a study using a French population of *A. ipsilon*, in which the first age of calling occurred significantly earlier under a photoregime of 16:8 (L:D) h (2.9 d) than under 12:12 (L:D) h (3.5 d) (Gadenne 1993). The magnitude of change in first age of calling was very small in both studies (0.15 d in our study and 0.6 d in Gadenne's), and therefore this factor alone cannot explain the changes in reproductive maturity observed under field conditions. Furthermore, such a small change could not be sufficient if we consider that the southward fall migration of *A. ipsilon* in North America (and probably other parts of the world) may take between 8 and 15 d (Showers 1997).

The analysis of pheromone and male response indicated that if photoperiod were the only factor controlling sexual receptivity, the percentage of insects mating would be lower during the long summer days than during the short days of spring and fall. Field data suggest that there is no reproductive diapause during the northward spring migration of *A. ipsilon.* The first females collected in the northern range in the spring are already mated and males are attracted in larger numbers to pheromone traps than to light traps (Willson et al. 1981, Kaster and Showers 1982, Levine et al. 1982, Clement et al. 1985). Furthermore, during the period of spring migration, most females caught in light traps in Louisiana, USA (an area where source migrants are likely to occur) are mated (Sappington and Showers 1992a). Some authors have indicated that the shift from a reproductive diapause to a normal reproductive stage could happen very soon after the migrating insects arrive at their destination, and they question the lack of reproductive diapause during the spring migration of *A. ipsilon* (Gatehouse and Zhang 1995, McNeil et al. 1995). However, indications of two different migratory strategies exist for at least two other migrant species: *P. unipuncta* and *Danaus plexippus* (L.) (see citations in McNeil et al. 1995). Given that the northward migration of *A. ipsilon* is faster than the southward migration (Showers 1997), it may not be optimal for the spring migrants to enter in a reproductive diapause stage, which could result in reduced lifetime reproduction (Zera and Denno 1997). The lack of response of *A. ipsilon* to photoperiod manipulation in the direction predicted by our hypothesis may be related to the observed asymmetry between the fall and spring migrations.

In *P. unipuncta* the first age of calling after emergence varies from 2 to10 d (Turgeon and McNeil 1982, Delisle and McNeil 1986). To reduce variability in the analysis of calling behavior, the authors grouped the individuals by "calling" age, where age 1 is the day that calling occurs for the first time. In *A. ipsilon*, >75% of the females have called by age 2, so we speculated that calling age and "chronological" age (where age 1 is the day of emergence) may produce equivalent results in this species. When analyzed using calling age, the onset times of calling for 12:12, 14:10, and 16:8 (L:D) h were 450, 361.11, and 302.5 min, respectively, after the onset of the scotophase, which is very similar to what we found using chronological age (Fig. 1). Using either method there was no phase-constancy with any of the photoperiodic cues tested. However, in *P. unipuncta*, females seem to be able to measure the absolute duration of either the photo- or the scotophase (Delisle and McNeil 1986). The analysis of percentages of calling using calling age produced similar results to those of chronological age reported in the results (photoperiod: $\chi^2 = 0.6$, df = 2, $P = 0.74$; age: $\chi^2 = 4.76$, df = 1, $P = 0.03$). For species like *A. ipsilon*, which do not show high variation in first age of calling, it may not be so critical which method of aging is used, but in species with high variability in first age of calling, such as *P. unipuncta*, the method of aging may be an important way to reduce variation.

In addition to photoperiod, temperature is the most likely factor responsible for reproductive diapause induction in insects. Under low temperature regimes, reproduction is delayed in several migratory insect species (Gatehouse and Zhang 1995). The first age of calling of *P. unipuncta* females reared under a photoregime of 16:8 (L:D) h at 10°C is 17.4 d, whereas those reared at 25°C start calling at 5.8 d of age (Delisle and McNeil 1987). The migration of *A. ipsilon* in North America normally takes place around the time of vernal and autumnal equinoxes, when temperatures are lower than in the summer. Temperature could be an important factor regulating the induction of reproductive diapause in *A. ipsilon.* Another factor that should be considered is the gradual shortening and lengthening of the days, which may produce different effects than constant photoperiods. The precalling period of *Mythimna separata* (Walker) is significantly longer in individuals reared under decreasing photoperiod and temperature conditions than in individuals reared under constant conditions (Han and Gatehouse 1991). At the latitudes and times of the year when *A. ipsilon* migrates, the photoperiod changes very quickly, as much as 1 h in 45 d, the same number if days it takes this insect to develop form egg to adult at 26°C (Harris et al. 1962). *Agrotis ipsilon* may show a stronger response to dynamic photoperiods than to constant photoperiods.

Conditions experienced by the immature stages will influence the amount of energy reserves transferred to the adults and therefore affect their migratory and reproductive potential. Larval density does not affect the rate of reproductive maturation (i. e., number of chorionated eggs) or flight behavior of *A. ipsilon* (Sappington and Showers 1992a, 1992b). Starvation of larvae and adults does not influence the propensity of *A. ipsilon* to engage in long duration flights or the duration of these flights (Sappington and Showers 1993). The individuals in our study were reared under the treatment photoregimes throughout their entire life cycle. However, we did not observe obvious changes in larval growth rate or adult weight (C.G., unpublished data), or in adult longevity (insects reared under 12:12, 14:10, and 16:10 [L:D] h lived on average 10.00 ± 0.33, 10.31 ± 0.32, and 10.21 ± 0.31 d, respectively; $F = 0.25$; df = 2, 278; $P = 0.78$) in relation to the changes in photoregime. The stage, or stages, that were sensitive to the photoregimes and resulted in the small differences in reproductive behavior were not determined in this study. In *P. unipuncta*, the temperature conditions experienced by the pupal stage are reflected in differences in the onset of calling behavior of the adult females (Turgeon and McNeil 1983). Age-dependent photoperiodic sensitivity can be an important source of variation in the induction of migration and diapause in insects (Spieth 1995).

The absence of larval host plant stimuli is an important factor triggering delayed reproduction in adults of several moth species (McNeil and Delisle 1989, Pittendrigh and Pivnick 1993, Tamhankar 1995, McNeil et al. 1995), and this could be a possible, although unexplored, factor in the induction of reproductive diapause of *A. ipsilon.* Geographic variation in the prereproductive period has been described for other moth species and for insects from a range of taxa (Gatehouse 1997). Under similar photoperiod and temperature conditions, females of a nonmigratory population of *P. unipuncta* from the Azores Islands have an earlier onset of reproduction than females from a migratory population from Canada (McNeil et al. 1995). Field populations of *A. ipsilon* are probably composed of individuals that vary in their response to environmental factors (Druzhelyubova 1976, Ayrepetyan 1983, Showers 1997). It could be argued that our test insects originated from a population with low propensity to migrate; however, studies using other populations of *A. ipsilon* report similar levels of variation in first age of calling as the ones reported in this study (Swier et al. 1977, Gadenne 1993).

The oogenesis-flight syndrome is a widely accepted theory that explains the developmental interaction between reproductive and migratory traits in insects, but concern about its power of prediction has been raised by a number of authors (Sappington and Showers 1992a, McNeil et al. 1995). For example, *D. plexippus*, *A. ipsilon,* and *P. unipuncta* show two annual cycles of migration, the fall migration is associated with reproductive diapause, but the spring migration apparently is not. In addition, some insects seem to reproduce before they migrate (Gatehouse and Zhang 1995). The adaptive significance of using two different reproductive strategies during migration is a question of great interest and deserves further study. However, a better understanding of the factors that govern reproductive diapause is also necessary. Future studies on *A. ipsilon* reproductive diapause should take into consideration other environmental stimuli, such as temperature, and gradual changes in photoperiod length and the possible existence of population variation in reproductive and migratory strategies.

Acknowledgments

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