Hormonal control of sexual behaviour in moths that migrate in response to predictable or unpredictable habitat deterioration

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Introduction

The use of insect sex pheromones as part of ecologically acceptable programs for the management of certain insect pests has not always lived up to initial expectations, due in part to a lack of thorough understanding of the communication systems we are attempting to exploit (Tumlinson 1988; McNeil 1991). A long-term programme was started over 10 years ago at l'Université Laval to study the behavioural ecology of pheromone-mediated mating systems of several economically important moth species, with a view to improving the effectiveness of pheromones as a management tool. The scope of the program was subsequently enlarged when it became apparent that this approach may also provide an avenue through which a better understanding of moth migration may be acquired (McNeil 1986). Therefore, the pheromone ecology of several migrant moth species is presently being studied to determine (*i*) the cues that initiate migration, (*ii*) the effect of these cues on behaviours associated with pheromone-mediated mating, and (*iii*) the underlying endocrinological processes that govern the observed behavioural changes. The species selected for study have very different life histories and migrate in response to either predictable or unpredictable changes in habitat quality. In this paper we will consider two moth species, the true armyworm, *Pseudaletia unipuncta* (Haworth) (Noctuidae), and the sunflower moth, *Homoeosoma electellum* (Hulst) (Pyralidae), both agricultural pests that do not overwinter in Canada but establish populations each year through immigration (Arthur and Bauer 1981; McNeil 1987).

Pseudaletia unipuncta

The true armyworm occurs annually in northeastern North America and, in some years, causes considerable damage to a variety of agricultural crops and pasture grasses (Beirne 1971). However, the sporadic nature of epidemics has complicated the establishment of an effective management strategy and, for this reason, work was initiated on the pheromone biology to determine if a network of pheromone traps could provide an effective early warning system of potential outbreaks. When females are reared in the laboratory at 25°C and 16 h light : 8 h dark, ovarian development, pheromone synthesis, and the onset of calling generally occur several days after emergence (Turgeon and McNeil 1982; Delisle and McNeil 1987*b*; Cusson and McNeil 1989*b*), and a similar pattern is seen in male responsiveness to the female sex pheromone (Turgeon et al. 1983; Dumont and McNeil 1992). However, lower temperatures, short day lengths, or the combined effects of the two, significantly delay ovarian development, the expression of calling behaviour, or pheromone synthesis in females by as much as 2 weeks (Turgeon and McNeil 1983; Delisle and McNeil 1986, 1987*a*, 1987*b*; Cusson et al. 1990); under these conditions very few males complete the entire suite of upwind flight behaviour to a pheromone source in the 3 weeks following emergence (Turgeon et al. 1983; Dumont and McNeil 1992). Furthermore, in the field there is a significant decrease in both the proportion of mated females in the population and the efficacy of pheromone traps between the spring and fall flights (McNeil 1987). Based on these data, McNeil (1987) proposed the existence of a two-way migration for the populations observed in Quebec, a northward spring immigration and a southward fall emigration, as this species does not possess the capacity to enter a prolonged diapause and thus survive within the habitat until conditions improve (Fields and McNeil 1984; Ayre 1985). Both migrations would be initiated by sexually immature adults in response to low temperatures and short days (around 10°C, 12 h L : 12 h D) that serve as indicators of predictable habitat deterioration (Fig. 1). By undertaking the northward migration in the spring, adults would avoid the unfavourable high summer temperatures in the overwintering sites, while the southward one in the fall would permit individuals to escape the lethal winter conditions that occur in the geographic range occupied during the summer.

The data obtained on the pheromone ecology of *P. unipuncta*, particularly the close relationship observed between ovarian development, calling behaviour, and pheromone titers (Cusson and McNeil 1989*b*), suggested that this species would be an excellent model with which to test the hypothesis that the neuroendocrine control of pheromone production in Lepidoptera occurs in species where adults are long-lived and have periods of suppressed mating (Barth 1965). Allatectomy and hormone replacement therapy, together with ovariectomies, provided irrefutable evidence that juvenile hormone (JH) not only controls ovarian development in *P. unipuncta*, but also regulates pheromone biosynthesis and the expression of calling behaviour (Cusson and McNeil 1989*a*). In light of these results the rates of *in vitro* JH biosynthesis were determined in different-aged adults of both sexes at 25°C, 16 h L : 8 h D, and 10°C, 12 h L : 12 h D (Cusson et al. 1990, 1994*a*) to determine if the onset of sexual maturation under the different conditions was associated with JH production. Under the temperature and photoperiodic regime considered indicative of predictable habitat deterioration, the rate of JH biosynthesis in females was significantly lower than in individuals reared under favourable conditions (Fig. 1). After 10 days at 10°C, 12 h L : 12 h D,

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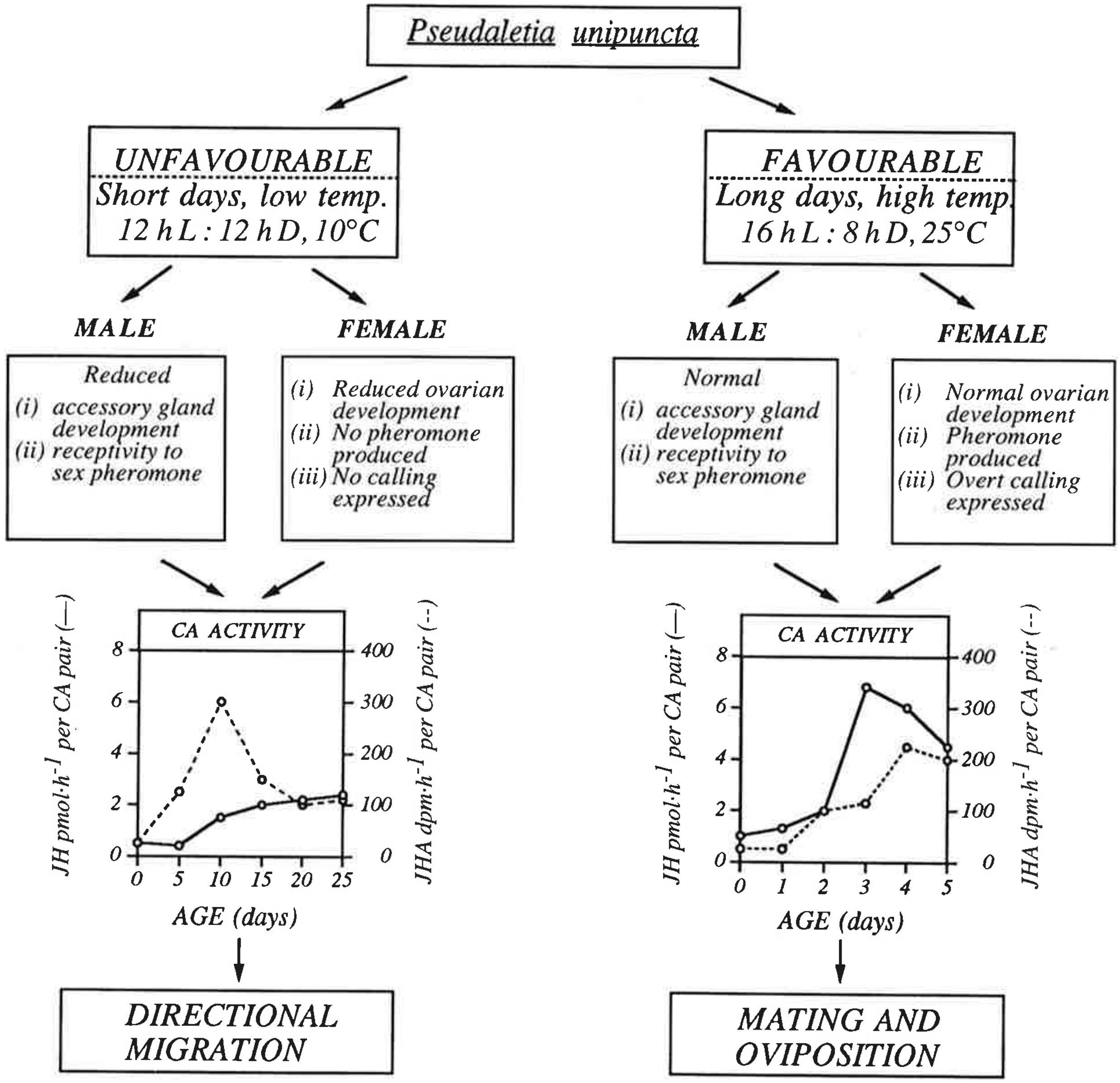

FIG. 1. Behavioural and endocrinological changes in *Pseudaletia unipuncta* adults reared under different temperature and photoperiodic conditions.

the age at which only the most precocious females called for the first time (Delisle and McNeil 1987*a*), the rate of JH synthesis was <50% of that observed after 3–5 days at 25°C, 16 h L : 8 h D (Fig. 1). Thus, JH production under the two rearing regimes follows the age-related temporal patterns of ovarian development, calling behaviour, and pheromone biosynthesis. The situation is somewhat different for males. While there is a clear relationship between the observed increase in male receptivity to the pheromone and the production of juvenile hormone acid (JHA) at 25°C, 16 h L : 8 h D, the same relationship is not evident at 10°C, 12 h L : 12 h D. The delay in receptivity is initially accompanied by reduced rates of JHA biosynthesis for the first 5 days, although there is a peak on day 10 before a return to low levels thereafter (Fig. 1). The results suggest that sexual maturation in both sexes is associated with JH titers, although additional work is required to clearly understand the pattern of JHA biosynthesis when males are held under short-day, low-temperature conditions.

The corpora allata (CA) of female and male true armyworms produce the three major homologues of JH and JHA, respectively, so additional work was undertaken to determine if the relative proportions and quantities of the three homologues may be associated with the observed changes in reproductive behaviour in response to temperature and photoperiodic cues (Cusson et al. 1993). In females the relative production of the homologues is JH II > JH I > JH III, with JH III remaining at low levels at all ages under both rearing conditions. Furthermore, the ratio of JH II/JH I increases as the overall biosynthetic activity of the CA increases, which generally coincides with the onset of reproductive activity. It is of interest to note that JH I and JH II are significantly more effective than JH III in stimulating vitellogenin accumulation in female armyworms (Cusson et al. 1994*b*). There were significant differences in the relative abundance of JHA and, as with females, the C_{17} and C_{18} homologues were always much more abundant than the C_{16}, regardless of rearing conditions. However, at 25°C, 16 h L : 8 h D, it is JHA I production that exceeds that of JHA II, while at 10°C, 12 h L : 12 h D, they are produced in approximately equal proportions. Considerably more experimentation must be carried out to determine if the different JH and JHA homologues or their ratios have specific functions associated with sexual maturation and pheromone production in females, as well as responsiveness to sex pheromones in males.

Homoeosoma electellum

The sunflower moth is a more specialised herbivore than the true armyworm, feeding on the flowers of a limited number of composites (Teetes and Randolph 1969*b*; Beregovoy 1985). Females preferentially oviposit in sunflower heads 2–4 days after the inflorescences have opened (Teetes and Randolph 1969*a*; DePew 1983), a choice that is modulated by the presence of oviposition stimulants in the pollen (Delisle et al. 1989). Pollen also influences the expression of calling behaviour, with females calling at a significantly younger age in the presence of pollen than in its absence (McNeil and Delisle 1989). The ability of females to select plants with pollen is of considerable importance for larval survival, as neonate larvae are unable to penetrate the unopened anthers (because of mechanical barriers and the presence of certain secondary plant compounds) and will starve to death if free pollen is not available (Rossiter et al. 1986). However, owing to the action of pollinators and abiotic factors, such as wind and rain, the presence of pollen on any given plant is ephemeral, and the time window during which a flower is an acceptable oviposition site is quite narrow. McNeil and Delisle (1989) proposed that the presence or absence of pollen would provide information on habitat quality, and the lack of suitable host plants would result in emigration (Fig. 2A). It is unlikely that there is a directional component to migration (e.g., north or south), as seen in the armyworm, for there is no compelling ecological reason to expect a greater availability of suitable oviposition sites in one direction over another in nature.

We have yet to examine how the presence or absence of pollen modifies the endocrinological processes governing the onset of sexual maturation in female sunflower moths, but we predict that it will be similar to that observed in the true armyworm (Fig. 1). One strong argument in support of this assumption is the observation that, as seen in *P. unipuncta* (Cusson and McNeil 1989*b*), the degree of ovarian development on the first day of calling is very similar among females regardless of their age (McNeil and Delisle 1989). Thus, in the absence of pollen we predict that there will be a lower rate of JH biosynthesis, resulting in the emigration of immature females from the habitat. There is a certain nuance in this species, possibly associated with the unpredictable nature of habitat deterioration, as in the absence of pollen some females initiate calling within 24 h of emergence. However, during the next 48 h the number of mature eggs in these females does not increase beyond ≈40, the number observed in all females on their first day of calling. As this is significantly different from the doubling observed in similar-aged females having access to pollen, McNeil and Delisle (1989) suggested that this is an adaptation to facilitate emigration for mature females, leaving habitats without suitable oviposition sites, by reducing the cost of flight. Selection experiments have shown that there is a significant genetic component to the age of first calling (J.N. McNeil, unpublished data), and the possibility that the patterns of JH biosynthesis differ between early- and late-selected lines will be investigated. If this is the case, this would be an excellent working model to compare intraspecific migratory potential in immature and mature individuals responding to the same environmental cues.

In contrast to the armyworm, the sunflower moth has the capacity to enter diapause and does so as a late larval instar, in response to short-day, low-temperature conditions (Chippendale and Kikukawa 1983; Kikukawa and Chippendale 1984). This provided an excellent system with which to examine the possible interaction between cues indicating the approach of seasonal habitat deterioration and those associated with unpredictable change in habitat quality on female calling. The difference in mean age of calling reported in the presence or absence of pollen at 25°C, 16 h L : 8 h D (McNeil and Delisle 1989) was also observed at 15°C, 16 h L : 8 h D, but there was no effect of temperature on the age of first calling (J.N. McNeil and J. Delisle, unpublished data). However, a photoperiodic effect was noted when the experiment was carried out under long- and short-day conditions, the difference in the mean age at the onset of calling between the pollen and no-pollen treatments being significantly less at 12 h L : 12 h D than at 16 h L : 8 h D (Fig. 2B). If, as we suggested above, calling is associated with JH titers, then short-day conditions stimulate JH biosynthesis, and this cue is considerably stronger than the inhibitory effect of the absence of pollen. Masaki (1978) reported that the development time from egg to adult in the univoltine cricket *Teleogryllus emma* Ohmachi and Matsumura was significantly shorter under short-day than long-day conditions at the same temperature. He suggested that this difference in development rates according to photoperiodic conditions was an adaptation permitting the animal to reach sexual maturity at the appropriate time in the fall to produce diapausing eggs. McNeil and Delisle (1992) suggested that accelerated sexual maturation in female sunflower moths under short-day conditions is also an adaptation associated with the seasonal synchrony of diapause. The underlying assumptions are that (*i*) by mating rapidly following emergence females could increase the probability that their progeny will complete larval development and enter diapause before habitat quality declines, and (*ii*) the increased survival of progeny would more than offset the increased cost of flight incurred by mature females searching for suitable oviposition sites.

Concluding remarks

The information obtained to date provides convincing evidence that the different developmental and behavioural aspects of the reproductive biology of the adult true armyworm are modulated by JH production. Furthermore, we believe that the delays observed under short-day, low-temperature conditions are associated with migratory behaviour in response to seasonal changes in habitat quality. Whether the delay in reproduction provides a larger time window during which adults may migrate in search of habitats suitable for reproduction (Delisle and McNeil 1987*a*) or facilitates the preparatory phase prior to the initiation of migration (McNeil et al. 1994) remains to be determined. In either case, we believe that migration is undertaken by both sexes and is initiated by sexually immature adults, thereby conforming with the oogenesis–flight syndrome (Johnson 1969). However, in species that initiate migration as sexually immature adults it is possible that as a result of the increase in body temperature associated with sustained flight, sexual maturation may occur before the migratory phase is terminated (McNeil et al. 1994), a possibility that will be examined.

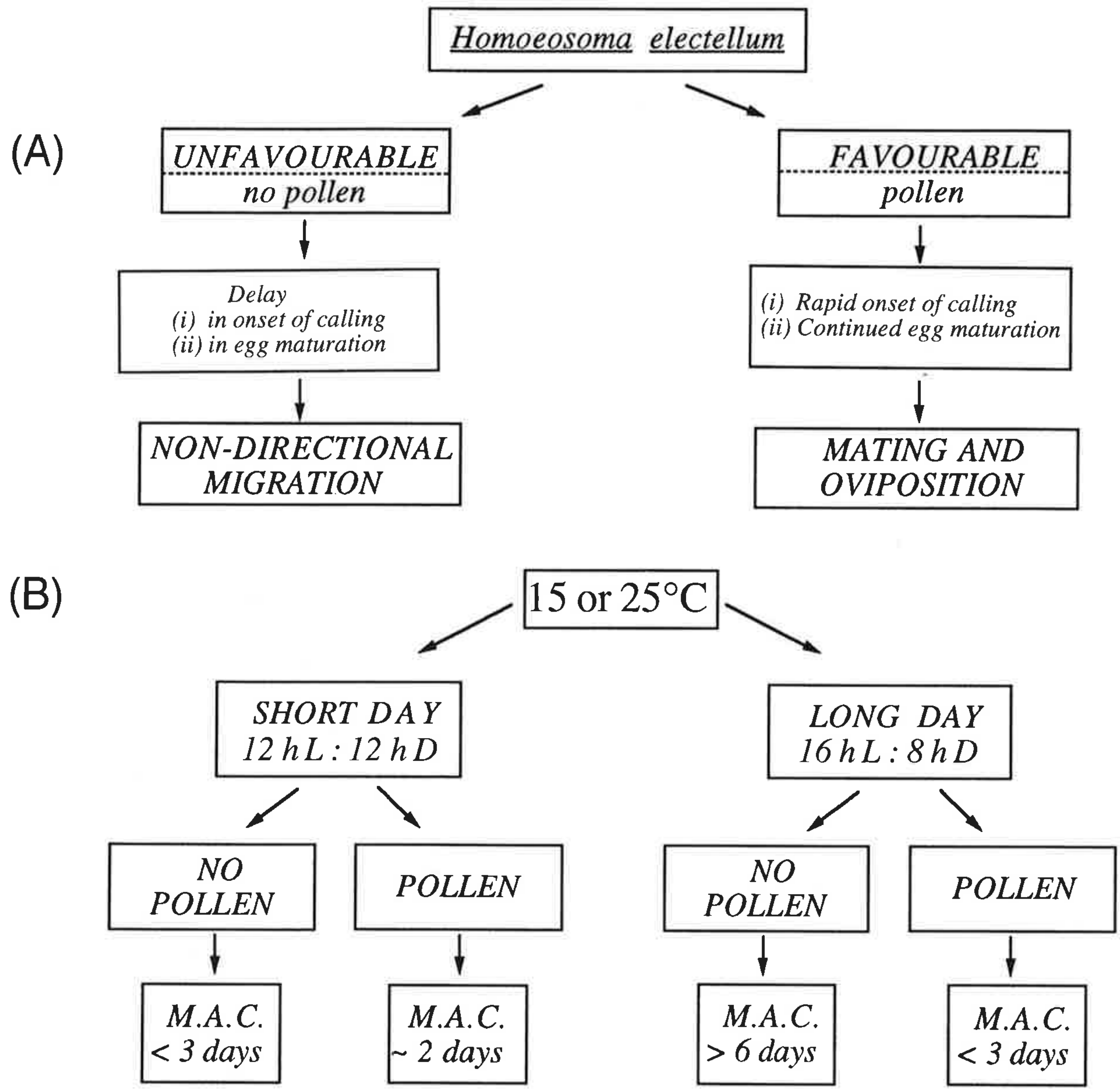

FIG. 2. Effect of the presence or absence of host-plant pollen on the calling behaviour and ovarian development of *Homoeosoma electellum* females at 25°C, 16 h L : 8 h D (A), and the mean age of calling for females held under long- and short-day photoperiodic conditions at either 15 or 25°C (B).

The data obtained with the sunflower moth suggest that migration may be undertaken by both immature and mature females in this species, a possibility that will be further investigated through our ongoing endocrinological studies comparing the relative importance of different cues associated with habitat quality. We also plan behavioural and physiological studies to determine if there is a relationship between sexual maturation and responsiveness to the female sex pheromone in the sunflower moth. In order to cover the entire spectrum of possible migration scenarios, the underlying endocrinology of reproduction in the spruce budworm, *Choristoneura fumiferana* (Clem.), is also being examined, for in this species migration is usually undertaken by mated females (Greenbank et al. 1980).

The idea that the oogenesis – flight syndrome does not fit all cases of insect migration has been accepted for some time (Rankin et al. 1986) and it is quite evident that data from a diversity of species deploying different migratory strategies must be gathered if we are to understand the endocrinological changes associated with behaviours exhibited during the different phases of the migratory process.

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