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**MIGRATION IN MOTHS: A PHYSIOLOGICALLY COORDINATED
HAPPENING OR JUST CASTING ONES FATE TO THE WIND?**

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ABSTRACT. Preliminary models describing the physiological changes associated with the initiation of migratory flight of the true armyworm, Pseudaletia unipuncta, and the spruce budworm Choristoneura fumiferana, are presented. Ovarian development, pheromone biosynthesis and the expression of calling behaviour (associated with the release of the sex pheromone) in the true armyworm all require juvenile hormone (JH). When reared under low temperature, short day conditions JH biosynthesis is low, resulting in a delay in sexual maturation and stimulating the onset of migration by immature adults. A similar scenario is proposed for the male responsiveness to the female sex pheromone. In contrast, spruce budworm migration is generally undertaken by mated females that have already laid a certain proportion of their eggs. In this species we hypothesize that the physiological processes involved in the expression of migratory behaviour are also related to changing JH titers but associated with male quality, determined by the quality of foliage available during larval development. High quality males transfer resources to the female at the time of mating that render her refractory and normal egg laying behaviour occurs. In contrast, if male resources are insufficient then JH titers remain low, calling behaviour resumes and females, stimulated by the high levels of ambient conspecific pheromone, initiate migration.

1. INTRODUCTION

All insect species are subject to predictable and unpredictable fluctuations in habitat quality and thus require life history traits that permit survival during periods when conditions are inappropriate for growth and reproduction. The reproductive options available in response to habitat deterioration may be considered with respect to time (now or later) and space (here or elsewhere), providing two broad categories, the "here-later"

and the "elsewhere-now" (Southwood, 1977; Solbreck, 1978). In the former, species respond to deteriorating conditions by entering a state of dormancy or quiescence somewhere within the habitat and remaining there until local conditions improve at some later date. In the second scenario, individuals in an appropriate stage of development emigrate in search of more suitable habitats where reproduction may continue. To date, considerably more attention has been given to species that exhibit "here-later" approaches (e.g. Tauber et al., 1986; Danks, 1987; Lee and Denlinger, 1991) undoubtedly due, in large part, to the inherent difficulties of working with small animals that may move distances of hundreds of kilometers in very short periods of time. However, there is an ever-growing body of literature describing the different facets of the "elsewhere-now" strategies associated with insect migration (e.g. Dingle, 1978; Rabb and Kennedy, 1978; Danthanarayana, 1986; Drake and Gatehouse, in press) and it is evident that there are many similarities in the endocrinological changes associated with migration and dormancy.

One major aspect that must be considered when examining the physiological changes occurring in the preparation for migratory flight in moths is the reproductive state of the adults at the time they migrate. Johnson (1969) proposed the "oogenesis-flight syndrome", where migration and reproduction are considered mutually exclusive processes, so that migration is undertaken either by sexually immature individuals or mature adults between reproductive cycles. However, it is now clear that the relationship between reproduction and migration varies considerably both inter- and intraspecifically (Pener, 1985, 1991; Rankin, 1989, 1991; Rankin et al., 1986), and that "oogenesis-flight syndrome" cannot be applied as a general rule for all migration (Rankin et al., 1986, Sappington and Showers, 1992).

To compare the physiological changes associated with the initiation of migration, we present preliminary physiological models for the true armyworm (migration by sexually immature adults) and the spruce budworm (migration by mated females).

2. *PSEUDALETIA UNIPUNCTA*

True armyworm populations occur annually in northeastern North America and in certain years may cause considerable crop losses. However, it has been clearly demonstrated that this species cannot overwinter in northern part of its summer range (Ayre 1985; Fields and McNeil, 1984) indicating that the populations observed are established through annual immigration. This insect is a sporadic agricultural pest, so following the identification of the female sex pheromone (Hill and Roelofs, 1980; McDonnough et al., 1980) a research programme on the pheromone ecology of *P. unipuncta* was initiated at Laval University. Studies of female calling behaviour (the

behaviour associated with the release of the sex pheromone) clearly demonstrated that the age of first calling was dependent upon prevailing temperature and photoperiodic conditions (Turgeon and McNeil, 1983; Delisle and McNeil 1986; 1987), with female reared under low temperature-short day conditions being significantly older than those under high temperature-long day ones. Similar patterns have been observed with male responsiveness to the sex pheromone (Turgeon et al., 1983; Dumont and McNeil 1992). At 25°C the expression of calling behaviour and onset of pheromone synthesis are closely associated with a certain stage of ovarian development (Cusson and McNeil 1989a), and all three are dependent on the presence of juvenile hormone (JH) (Cusson and McNeil, 1989b). A similar scenario has been proposed with respect to male maturation and the receptivity to the female pheromone (Cusson et al, 1993; Dumont and McNeil, 1992). Additional studies on the reproductive physiology confirmed that the delay in both male and female maturation under low temperature-short day conditions are accompanied by lower levels of JH biosynthesis (Cusson et al., 1990) and that the ratios of the different JH homologues (JH acids in the case of males) vary somewhat under different rearing conditions (Cusson et al., 1993).

Trapping with pheromone and light traps McNeil (1987) found that during the immigrant flight females were mated and males responded to synthetic pheromone lures. However, females captured in the fall were generally unmated, and possessed large fat bodies but with very little evidence of ovarian development. Similarly males, while present in light traps, were not found in pheromone traps. Thus, both under laboratory and field conditions, there is a delay in the onset of reproduction when adults are subjected to cues associated with the approach of winter (predictable habitat deterioration) in the summer range of *P. unipuncta*. A model for the physiological changes associated with either reproduction or flight in the true armyworm, similar to that proposed for the milkweed bug by Rankin and Riddiford (1978), is presented in Figure 1. The same low temperature, short day conditions could also serve as cues of habitat deterioration during the spring at overwintering sites, where the prevailing summer temperatures detrimentally affect larval survival and reproduction (McNeil, 1987).

It has been suggested that the extended precalling period observed when moths are reared under conditions associated with predictable habitat deterioration provides a wider time window for migration to occur (Delisle and McNeil, 1987; McNeil, 1987; Han and Gatehouse, 1991a, b; Hill and Gatehouse, 1993). However, as pointed out by McNeil et al. (in press), body temperatures increase considerably during flight so once migration is initiated ambient temperature conditions would not be a major parameter affecting the precalling period unless there are physiological mechanisms that compensate for thermal increases by inhibiting JH biosynthesis. If the actual window available for migration once flight is initiated is independent

of temperature, why would temperature have such a significant effect on the precalling period in certain migrant moth species? McNeil et al. (in press) have suggested two ways in which the observed delay in maturation at low temperatures may be a preflight adaptation of benefit to migrants. Adults must feed in order to accumulate the necessary resources for sustained flight and in the fall the number of available nectar sources may be limited. Thus a delay in maturation could provide the foraging time necessary to locate food sources without reducing the length of the time subsequently available for the actual migration. Similarly, any delay in the initiation of migration associated with unfavorable climatic conditions would not significantly reduce the migratory window if the rate of sexual maturation during this time was markedly reduced.

3. *CHORISTONEURA FUMIFERANA*

The spruce budworm is a cyclic species and under natural conditions (in the absence of intensive control programs) population outbreaks occur about every 30 years (Royama, 1984). During the epidemic phase, which may last several years, there is an evident decline in foliage quality and migration from deteriorating sites has been well documented (Greenbank et al., 1980). In this species the majority of migrants are mated females that have already laid a certain proportion of their total egg complement, so the model proposed for species such as the true armyworm (Figure 1) certainly would not hold. An ongoing study of spruce budworm reproduction has shown that the quality of food obtained by males during larval development markedly affects several aspects of female reproduction (Hardy and Delisle, 1992). Diet-reared females mated with males reared on limited, poor quality, foliage produced significantly fewer fertile eggs in the 48 h following mating than those mated with males reared on good foliage. Furthermore, they were more likely to resume calling and remate. It has been suggested that one cue used to initiate migration is the ambient pheromone titer as (i) spruce budworm females are able to detect the female sex pheromone (Palaniswamy and Seabrook, 1978, 1985), and (ii) in the first two days following mating, mated females exhibit increased flight activity when in the presence of high ambient concentrations of the pheromone (Sanders, 1987). McNeil et al. (in press) proposed that, as females may receive resources other than sperm at the time of mating that influence egg production and oviposition (Friedel and Gillott, 1977; Loher et al., 1981), female longevity and fecundity (Gwynne, 1984; Royer and McNeil, 1993), as well as female receptivity (Svard, 1985; Young and Downe, 1987; Mbata and Ramaswamy, 1990), male quality could modify female JH titers and be a determining factor in the decision to migrate or not. The model proposes (Figure 2) that, in declining habitats, females will have lower levels of JH synthesis due to the poor male quality. Palaniswamy and Seabrook (1979; 1980) reported that topical application of JH analogs reduced female sensitivity to the sex pheromone so females

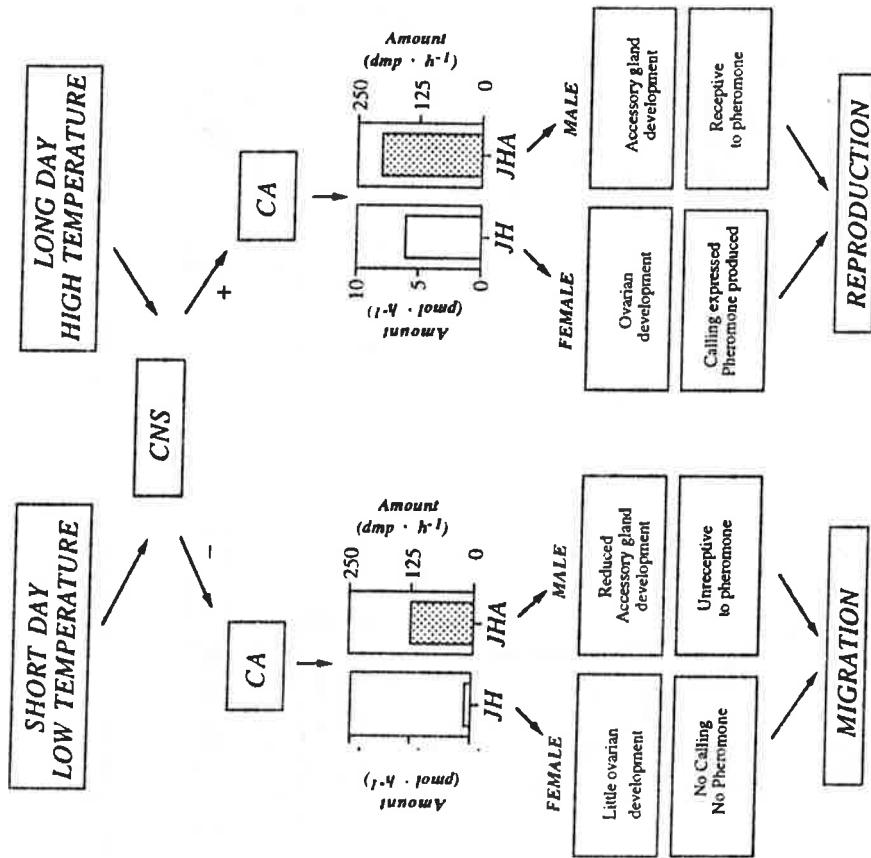


Figure 1. A model of physiological processes associated with the initiation of reproduction or migration by sexually immature adults of the true armyworm, *Pseudotelia unipuncta*.

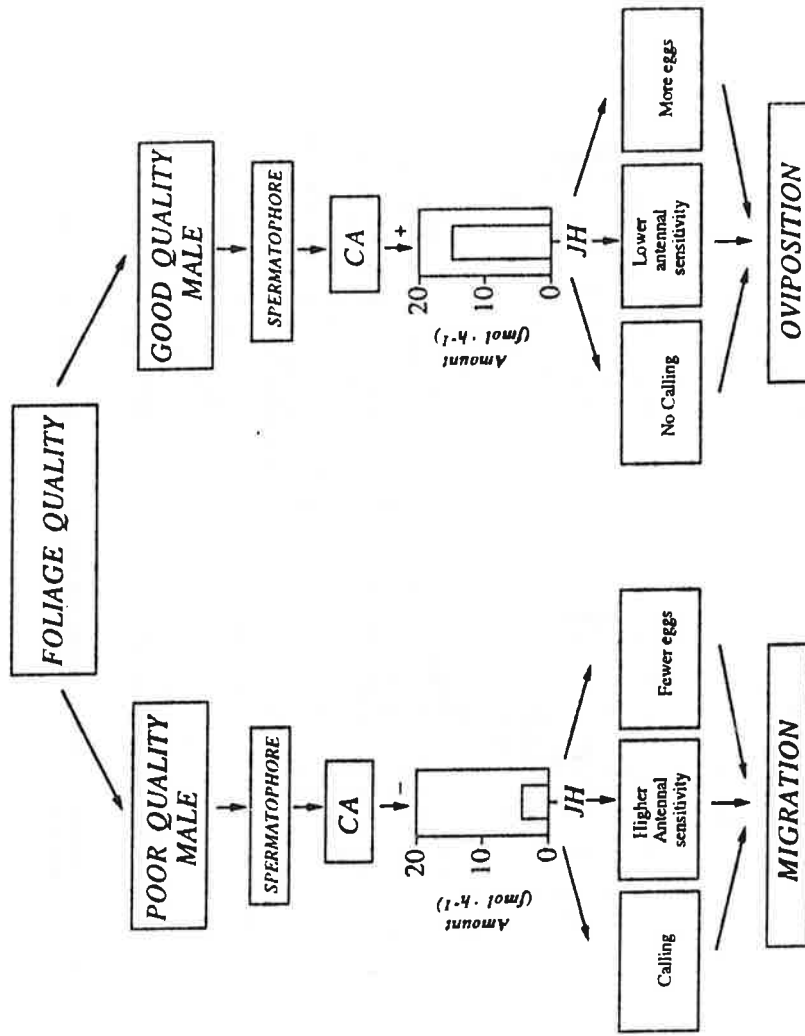


Figure 2. A model of the physiological processes associated with continued oviposition or migration by mated females of the spruce budworm, *Choristoneura fumiferana*

with low JH titers may be very sensitive to ambient pheromone levels which, due to the high proportion of individuals calling following first mating, would be high concentrations. Under such conditions females will have a higher tendency to migrate than when mated with high quality males in stands where levels of ambient pheromone are low. In addition, the lower JH titers may slow down egg maturation and stimulate migratory flight, in a manner similar to that proposed in true armyworm model, but on a much shorter time scale. Preliminary data indicate that following mating JH production by females is affected by male quality (Cusson and Delisle, unpublished).

4. CONCLUDING REMARKS

It is evident that the two models proposed, which may represent the extremes of the spectrum of migratory strategies deployed by Lepidoptera, are far from complete and considerably more work on both species is required to verify and elaborate on the proposed processes. For example, a comparison of the physiological profiles of males and virgin females are essential in order to understand why migratory flight is usually undertaken by mated spruce budworm females. Since McNeil (1986) hypothesized that female calling behaviour could be a useful parameter to identify moth species that migrate as sexually immature individuals, a number of studies have shown that the mean calling age in known migrant species is significantly affected by the presence or absence of cues associated with predictable and unpredictable changes habitat quality. For example, the length of the precalling period of *Autographa gamma* (Hill and Gatehouse, 1993) and the Oriental armyworm (Han and Gatehouse, 1991a, b) is affected by seasonal cues such as temperature and photoperiod while unpredictable cues, such as the presence or absence of suitable host plants, determines the age of first calling in the sunflower moth (McNeil and Delisle, 1989) the diamond back moth (Pivnick et al., 1990) and the corn earworm (Raina et al., 1992). However, to date very few studies have examined the underlying physiological processes associated with these changes in calling behaviour and the general applicability of the true armyworm model (Figure 1) must be verified. Furthermore, the extent to which the budworm model holds for other species known, or thought, to migrate as sexually mature or mated individuals must be determined. It is conceivable that some species have characteristics of both models. For example, while the monarch butterfly initiates its fall, southward migration as sexually immature individuals, the northward, spring migration may be undertaken by adults that mated at the overwintering site (Brower, 1985). Therefore, in order to obtain a broader understanding of the different processes and to develop more general models, we need a number of comparative studies on species that not only migrate in different reproductive states but also respond to an array of abiotic and biotic factors to initiate migratory behaviour. This latter point is important as adaptations

associated with unpredictable habitat deterioration are generally less likely to involve long-term neuroendocrine changes than those associated with seasonally predictable ones (Tauber et al., 1986). This may explain why, under conditions favorable for reproduction, sexual maturation in the sunflower moth that migrates in response to the unpredictable availability of suitable host plants (Arthur and Bauer, 1981) only requires about 2 days following emergence (McNeil and Delisle, 1989) but yet takes an average of 6 days in the true armyworm (Turgeon and McNeil, 1982), a species that migrates to avoid predictable seasonal habitat deterioration

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