CHAPTER 1 GENERAL INTRODUCTION

1.1 Environmental influences on insect flight and migration

Flight is a key component of insect life-histories (Johnson 1969, Dingle 1985, 1986, 1989, Gatehouse 1989, Tauber *et al.* 1986). Insect flight may involve movement within a habitat for such activities as feeding, mating or oviposition. These flights have been termed 'appetitive' (Provost 1952), 'trivial' (Southwood 1962), or 'vegetative' (Kennedy 1961, 1975). In contrast, migratory flights take insects beyond their habitat, allowing escape from unfavourable conditions and colonisation of new habitats (Johnson 1969, Dingle 1985, 1986, Tauber *et al.* 1986). At a behavioural level, migratory flights are characterised by the suppression of responses to stimuli which would normally localise activity within habitats for reproductive purposes (Kennedy 1961, 1975).

Insect flight may be influenced by genetic (polymorphic) and environmental (polyphenic) factors (Dingle 1985, 1986, 1989, Gatehouse 1986, 1989). How environmental factors influence an insect's flight behaviour will depend on a suite of species-specific physiological and morphological traits, and on the reliability of environmental cues as predictors of impending habitat change.

Many insects display age-related changes in flight and reproductive behaviour (Johnson 1969, Dingle 1985, Rankin *et al.* 1986). The sequence of these changes will depend on an insect's life history strategy. For some insects there is a temporal separation of flight and reproduction. For example, in the noctuid moth, *Spodoptera exempta*, migratory flights appear to be restricted to within 1 - 2 nights of emergence and prior to the onset of reproduction (Riley *et al.* 1983, Gatehouse 1986). Johnson (1969) termed this type of behaviour an oogenesis-flight syndrome. In contrast, other insects display coincident increases in flight activity and reproduction. In the tortricid, *Epiphyas postvittana*, the development of flight capacity is well synchronised with the build-up and decline of reproductive capacity (Gu & Danthanarayana 1990). Similarly in the noctuid, *Agrotis ipsilon*, tethered flight studies suggest synchronisation of flight ability and reproductive development (Sappington & Showers 1992). Such species may display inter-reproductive migratory flights.

The sequence of age-related changes in flight and reproduction may be modified by factors such as the availability of mates and adult food sources. Tethered flight studies of *H. armigera* by Armes & Cooter (1991) indicate that successful mating suppresses subsequent flight activity and enhances reproductive output. In the pyralid, *Chilo partellus*, however, mating has been shown to enhance flight activity (Pats & Wiktelius 1989). If adults require carbohydrates for reproductive development, the lack of a food source during early adult life may promote flight. Hackett & Gatehouse (1982) found that *H. armigera* moths starved during the first two days of adult life exhibited longer tethered flights than corresponding fed moths.

Further, larval food quality and quantity may influence flight through its effect on body size parameters and reproductive performance (Slansky & Scriber 1985, Slansky & Rodriguez 1987). Danthanarayana (1976) demonstrated increased flight (migratory) activity among *Epiphyas* moths subject to reduced or low quality larval food. Poor larval nutrition has also been suggested to induce long flights in *H. armigera* moths (Hackett & Gatehouse 1982).

There is often an interaction between flight and reproduction that may entail both costs and benefits (Rankin *et al.* 1986, Dingle 1989, Gatehouse 1989). Flight is energetically expensive (Casey 1989). Although energy consumption is normally compensated for by feeding, energy consumption during extended flights may be such that the availability of energy for reproductive purposes may be affected. Reductions in fecundity following long duration (migratory) flights in the laboratory have been demonstrated in the dipteran, *Oscinella frit* (Rygg 1966) and in at least one noctuid species (Gunn *et al.* 1988). Other studies, however, have shown that flight may stimulate reproduction. Rankin *et al.* (1986) provide data for three highly migratory species, *Oncopeltus fasciatus, Hippodamia convergens* and *Danaus plexippus,* showing that performance of long duration flight resulted in acceleration of reproduction and enhanced reproductive output.

The efficiency of a flying insect to move within, and to traverse between, habitat patches will be subject to the biomechanical (Pennycuik 1972) and bioenergetic (Roff 1991) constraints of flight. For geometrically similar animals, biomechanical and bioenergetic models predict that flight performance (flight speed and distance flown) will be positively correlated with body size. Large, fast flying insects maintain a deeper effective flight boundary layer (*sensu* Taylor 1974) than smaller, slow flying insects (Taylor *et al.* 1979). Hence relatively large insects such as noctuid moths will be better able to control their preferred direction of movement relative to the direction of the wind; they are consequently more capable of carrying out the vegetative (*sensu* Kennedy 1975) movements required for feeding, mating and oviposition.

For most nocturnal insects, environmental temperature is the principal abiotic factor limiting the timing of flight activity. All insects display a minimum flight threshold below which flight is impossible. For example, Lingren *et al.* (1986) report that nocturnal activity of *H. virescens* ceases once ambient temperature drops below 10 ^{o}C. Hsaio (1978) in a study of the circadian activity of *H. zea* moths under varying temperature regimes, determined that at low temperatures (10 - 15 ^{o}C) activity was restricted to the first half of the night. Whereas , at higher temperatures flight activity increased and extended further into the night. Elevation of body temperature to a level at which flight is possible for nocturnal insects is accomplished solely by endothermic mechanisms of heat gain (May 1985). Body temperature may subsequently be regulated within relatively narrow limits, conferring benefits derived from increased habitat use both temporally and spatially, and improved flight and foraging ability (May 1985).

Environmental factors that trigger phenotypic changes in flight behaviour may be directly associated with changes in habitat quality or may act as token stimuli which herald a change in environmental conditions (Fraenkel & Gunn 1940, Dingle 1985, 1989, Tauber *et al.* 1986, Gatehouse 1989). For insects living within temperate zones, seasonal changes in temperature and photoperiod are considerable, and hence, act as reliable indicators of impending changes in seasonal conditions (Beck 1980, Tauber *et* *al.* 1986). There is a large body of literature documenting the influence of photoperiod, and to a lesser extent temperature, as cues which induce phenotypic changes in life-history traits that enhance migration (Tauber *et al.* 1986, Dingle 1985, 1989). Most studies (see references in Tauber *et al* 1986, Dingle 1989) have centred on species such as the hemimetabolous bugs, *Oncopeltus* and *Dysdercus*. Few examples exist for such highly mobile insects as noctuids. Studies of migratory noctuids, including *Heliothis*, *Mythimna*, and *Spodoptera* spp. from North America (various authors in Rabb & Kennedy 1979) provide no indication that migratory activity of these species is controlled by seasonal factors. More recently McDonald & Cole (1991) demonstrated that *Mythimna convecta* females subject to long daylengths (16:10, L:D) were slower to mature than females held under shorter daylengths. McDonald & Cole (1991) suggest that, as *M. convecta* is largely a pre-reproductive migrant, such a response may assist this species to emigrate from unfavourable habitats. Presumably mid-summer (long daylength) conditions bring about habitat deterioration for this species. They further suggest that seasonal changes in photoperiod may provide a cue to induce and/or prolong migratory activity.

Geographic variation in life history traits is ubiquitous. Patterns of geographic variation may result from recent adaptation to ecological conditions and from historical factors (Thorpe 1987). Geographic variation for migratory activity has been demonstrated in the bug, *Oncopeltus* (Dingle 1978, 1981). However, there are no studies known to the author which specifically examine geographic variation in migratory propensity among populations of noctuids or other Lepidoptera.

1.2 The biology and ecology of *Helicoverpa punctigera and H.armigera* in Australia

1.2.1 Taxonomy, distribution and pest status

Recent taxonomic studies (Matthews 1987, cited in Fitt 1989) have justified the use of the generic name *Helicoverpa* as first proposed by Hardwick (1965). *Heliothis punctigera* (Wallengren) and *H. armigera* (Hübner) consequently revert to the generic name *Helicoverpa,* as has the American species, *H. zea.* The generic name *Heliothis* has been retained for *H. virescens* (Matthews 1987).

H. armigera has a cosmopolitan distribution, being recorded from Africa, the Middle East, southern Europe, India and Asia (Fitt 1989). In Australia, *H. armigera* is widespread throughout eastern regions, occupying both coastal and inland areas, and in the north of Western Australia (Zalucki *et al.* 1986, Gregg *et al.* 1989). It is generally associated with regions that support summer crops. *H. punctigera* is endemic to, and common throughout, Australia.

H. punctigera and *H. armigera* are major pests of a wide range of agricultural and horticultural crops in Australia (Zalucki *et al.* 1986). Annual expenditure within Australia, arising from yield reduction, cost of chemicals and crop monitoring have been estimated at $25 million (Fitt 1989). Fitt (1989) listed the major high value crops attacked by both species; cotton, soybeans, tobacco and pulses (chick-pea and pigeon pea) account for most of the economic loss. For many crops, successful pest management depends heavily on the use of pesticides. Concomitant with the use of pesticides has been the development of insecticide resistance by *H. armigera* (Goodyer *et al.* 1975, Gunning *et al.* 1984). As yet *H. punctigera* has not developed resistance to any chemical. This has been attributed largely to differences in mobility, geographic distribution and host plant utilisation between the two species (Fitt 1989).

1.2.2 Ecology of *H. armigera and H. punctigera*

Several recent reviews have summarised much of the literature on the ecology of *H. armigera* and *H. punctigera.* Zalucki *et al.* (1986) provided a comprehensive summary of the biology and ecology of *H. punctigera* and *H. armigera* in Australia, covering taxonomy and identification, distribution and host plants, reproduction, development and survival of immatures, and population biology and dynamics. Farrow & Daly (1987) summarised evidence for and against the occurrence of long distance flights by *H. punctigera* and *H. armigera* adults. More recently, Fitt (1989) documented the ecology of *H. punctigera* and *H. armigera* in relation to agroecosystems, emphasising those factors that have allowed the genus to achieve major pest status. Each of these reviews have identified flight behaviour and the capacity for long distance flights as being central in determining the population dynamics of *H. punctigera* and *H. armigera*, and hence, identifying the major role of flight in the establishment and maintenance of their pest status. I will provide a brief summary of the known aspects of the flight behaviour of *H. punctigera* and *H. armigera* and emphasise those areas where our current understanding of flight behaviour of these species is incomplete or lacking.

1.2.2.1 Diel flight period

The phenology of nocturnal activity is well documented. Data from a number of sources, including light traps (Roome 1975, Persson 1976), radar studies (Drake & Farrow 1985) and visual observation (Roome 1975, Lingren *et al.* 1988, Topper 1987) have identified a period extending from dusk and into the first 4 hours of the night in which most feeding and oviposition occur. The initiation of migratory flights appear to be restricted to within an hour of sunset, although flight itself extends to dawn. A second period of activity in the latter half of the night involves mating (Roome 1975, Topper 1987). Though *H. punctigera* and *H. armigera* are primarily nocturnal, diurnal feeding and oviposition has also been recorded (Zalucki *et al.* 1986, Coombs 1992).

1.2.2.2 Seasonal phenology

H. punctigera and *H. armigera* are active in cropping areas in eastern Australia during spring and summer (Wardhaugh *et al.* 1980, Morton *et al.* 1981, Fitt *et al.* 1989). Differences in seasonal occurrence exist between the two species and are related to a combination of factors involving differing migratory and diapause strategies, distributions, range of utilised host plants and insecticide resistance (Farrow & McDonald 1987, Fitt 1989, Fitt & Daly 1990)

H. punctigera adults appear in cropping regions in eastern Australia during spring (September - October) (Zalucki *et. al.* 1986, Fitt *et. al.* 1989, Fitt & Daly 1990). Numbers of adults are greatest during this period, however, subsequent adult generations in this area are smaller and often absent by mid summer (Fitt *et al.* 1989, Fitt & Daly 1990), although numbers may be higher in southern Australia in summer and autumn. *H. punctigera* do not appear to enter an overwintering diapause in this area. Fitt & Daly (1990) were unable to locate diapausing *H. punctigera* pupae in the Namoi/Gwydir cropping region over two cropping seasons (1987 & 1988). Spring populations of this species thus appear to be derived largely if not wholly from immigrants. Evidence from extensive larval surveys and an adult trapping network has indicated that these moths may be derived from substantial winter breeding populations in inland regions of Australia where adults breed on native ephemeral hosts (Gregg *et al.* 1989).

H. armigera adults appear in eastern cropping areas during spring. The adult population size, as indicated by light and pheromone trapping, is typically greatest during this period (Zalucki *et al.* 1986, Fitt *et al.* 1989, Fitt & Daly 1990). Adults remain locally abundant throughout the remainder of the season, though numbers typically decline with progressive generations. Spring populations of *H. armigera* are derived from a combination of local individuals which have overwintered, as diapausing pupae, (Fitt & Daly 1990) and from immigrants (Farrow & Daly 1987). *H. armigera* pupae typically enter diapause during mid to late autumn, remaining in crop residues until spring. Survival of overwintering pupae is dependent on levels of parasitism and cultural practices (tilling crop residues destroys a high proportion of pupae) (Fitt & Daly 1990).

The fate of the late season *H. punctigera* populations in eastern cropping and pastoral zones is unclear. Populations may simply die out, though this is unlikely, as suitable host plants persist until early autumn (Wardhaugh *et al.* 1980, pers. observ.), though survival may be poor in a sprayed crop environment. In addition, the existence of a diapause pattern involving a facultative winter, and the possibility of a summer diapause, may also contribute to the decline in insect numbers (Fitt 1989). Emigration of adults from eastern regions during late summer and early autumn may also be a factor contributing to the decline in *H. punctigera* numbers. South-easterly winds and easterly sea-breezes are common at this time of year (Symmons 1986, Farrow & McDonald 1988). If migratory flights were to coincide with the occurrence of such winds, movement of adults westward would be possible. Such migratory movements may then contribute to the re-establishment of the autumn and winter breeding *H. punctigera* populations in inland regions (Gregg *et al.* 1989). At present there is no evidence indicating that this occurs, though other researchers (Farrow & McDonald 1987) have suggested similar movements of other noctuids to re-establish inland winter breeding populations.

1.2.2.3 Host plants

H. punctigera and *H. armigera* are highly polyphagous. Zalucki *et al.* (1986) record 161 plant species in 49 families as hosts. The majority of these hosts are exotic, comprising agricultural, horticultural and weed species. Only 3 native hosts have been recorded for *H. armigera,* and 25 for *H. punctigera.* Weeds and other non-cultivated hosts may play an important role in the early season establishment and build-up of *Helicoverpa* populations in cropping areas prior to crops becoming attractive (Fitt 1989). The suitability of non-crop hosts for larval development and survival, and adult reproductive and flight performance has not been investigated.

1.2.2.4 Flight and migratory activity

The existence of long-distance flights by *H. punctigera* and *H. armigera* adults is well documented (Farrow & Daly 1987, Fitt 1989). Evidence of migratory flights has been inferred from patterns of genetic variation (Daly & Gregg 1985), detection of resistant phenotypes in regions where host plants are unsprayed (Gunning & Easton 1989), and from light trapping and radar studies (Drake *et al.* 1981, Morton *et al.* 1981).

Farrow & Daly (1987) categorised flight activity by *Helicoverpa* spp into 3 broad groups; firstly, short-range flights occurring within or just above the crop canopy; secondly, long-range flights occurring within the insects' boundary layer; and thirdly, migratory flights occurring above the flight boundary layer, often at high altitude (c. 50 - 1000m).

The short-range flights occur in close proximity to the host crop, and involve the location of feeding, oviposition, and sheltering sites and mates. The long-range flights, as defined by Farrow & Daly (1987), occur at heights of up to 10 m and may involve distances of between 1 and 10 km. These flights are often downwind, and they involve movement between host crops to locate feeding and oviposition sites. The extent of these flights is governed by the spatial dynamics of suitable hosts and the flight speed of the adult.

In cropping systems the timing of these inter- and intra-crop movements in the biological boundary layer are well documented for *H. armigera* and other heliothine species. Typically, on the night of emergence, adults undertake a single flight of no more than 30 m, following a brief pre-teneral period (Lingren *et al.* 1988). On subsequent nights, extensive intercrop movement occurs during early evening involving males, and virgin and inseminated females (Topper 1987). This redistribution of moths occurs regularly (at least over the first 1 - 6 nights following emergence) and prior to oviposition behaviour on each night. In contrast, other studies have indicated that inseminated females remain within attractive (flowering) host crops (Roome 1975).

Though Hackett & Gatehouse (1982) examined aspects of age-related flight performance for *H. armigera* from the Sudan, and more recently Armes & Cooter (1991) undertook similar studies for *H. armigera* from India, no studies have examined age-related flight and reproductive performance for Australian populations for either *H. armigera* or for *H. punctigera*. The studies of Hackett & Gatehouse (1982) and Armes & Cooter (1991) established that the flight ability of *H. armigera* adults increases during early adult life, coincident with the onset of reproductive activity.

Radar studies suggest that migratory flights of *H. punctigera* and *H. armigera* may occur in the geostrophic wind at altitudes generally in excess of 150m with most migrants concentrated in a layer at the top of the thermal inversion generally between 200 - 400 m (Farrow & Daly 1987). Displacement under these conditions is governed by wind speed and direction and flight duration and orientation of the insect. Migratory flights among many insects are generally thought to be restricted to a post-teneral pre-reproductive phase (Johnson 1969). This has been assumed to be the case for *H. punctigera* and *H. armigera* (Farrow & Daly 1987).

Despite an increasing understanding of the role that flight at these varying levels plays in the population dynamics of *Helicoverpa* spp, much remains to be learned regarding the physiological or environmental cues that govern the timing and pattern of *Helicoverpa* flight. An understanding of the factors affecting the life-history performance including flight and migratory activity of *Helicoverpa* spp is essential for the development of accurate models (see Stinner *et. al.* 1983) that will allow the forecasting of the population build-up of these species.

In this thesis I examine the role of environmental factors in modifying the flight capacity of *Helicoverpa punctigera* (Wallengren) and *H. armigera* (Hübner) adults. Specifically, I address the following questions:

(1) What is the reproductive and mated status of migrant *Helicoverpa* spp ? (Chapter 2)

(2) What is the sequence of age-related changes in flight capacity and reproductive performance, and how are these modified by mating and the availability of adult food sources ? (Chapter 3)

(3) Does body size influence flight capacity ? (Chapter 4)

(4) Is there geographic variation in flight capacity? If so, do the differences reflect adaptation to the respective ecological conditions ? (Chapter 5)

(5) Do adults closely regulate body temperature and what are the minimum temperature thresholds for flight ? (Chapter 6)

(6) Does larval diet influence flight and reproductive performance ? (Chapter 7)

(7) Do seasonal changes in temperature and photoperiod act as cues for phenotypic changes in life history traits that enhance migration ? (Chapter 8)

In a final chapter (9) I draw together the conclusions from chapters 2 to 8 to answer these questions.

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CHAPTER 2

REPRODUCTIVE MATURITY AND MATING STATUS OF MIGRANT H. PUNCTIGERA and H. ARMIGERA

2.1 Introduction

There is a large body of literature documenting that migration occurs prior to the onset of reproduction for many insects (Johnson 1969, Dingle 1985). Migrant *H. punctigera* and *H. armigera* adults have similarly been assumed to be pre-reproductives (Farrow & Daly 1987). Attempts at direct sampling of migrating adults at altitude are difficult due to the low aerial densities of moths and have yielded few quantitative results (Drake & Farrow 1985). In addition, the physiological condition of adults trapped at ground level may represent individuals engaged in either vegetative or migratory flights (*sensu* Kennedy 1975), thus making the detection and characterisation of migrants difficult (Raulston *et al.* 1982). On occasions where immigration has been detected (for example, Vaishampayan & Verma 1987) *Helicoverpa* moths have been immature and unmated.

Data are presented here on the reproductive maturity and mating status of female *H. punctigera* and *H. armigera.* The adults were recovered from light-traps mounted on towers. The traps caught large numbers of moths in association with particular synoptic conditions (see Gregg *et al.* 1993). These moths are strongly suggested to be migrants.

2.2 Methods

Moths were trapped using a tower-mounted light trap located at Point Lookout (30° 29'S, 152° 28'E), New England National Park, north-eastern New South Wales. The trap was operated over a period of 4.5 yr, from November 1985 to March 1990. The surrounding vegetation is predominately *Eucalyptus* forest. Extensive pheromone trapping and larval surveys have not shown any evidence of local breeding of *Helicoverpa* spp. at this location (P. Gregg unpublished). The light was not visible from ground level and there were no other lights on the tower. The light trap was set at a height of approximately 49 m above ground level. Moths were trapped directly into 70 % alcohol and catches segregated into pre- and post-midnight fractions or at least nightly over the course of the study. Catches typically persisted for only one night and often over only half a night, and only rarely were catches in the post-midnight period followed by catches in the pre-midnight period of the next night (Gregg *et al.* 1993). Female moths were dissected and examined as soon as possible after the date of capture. Samples of moths were dissected on occasions where > 10 individuals (male and female total) were trapped and when catches of other insects suggested a migratory event had occurred (see Gregg *et al.* 1993).

Species identification of females followed Common (1953). Mating status was determined by counting the number of spermatophores in the copulatory bursa of each female. Reproductive status of females was compared with reproductive parameters of conspecific moths of known ages to enable characterisation of females as either immature or mature. For the latter purpose females of *H. punctigera* and *H. armigera* were dissected upon emergence and at 24, 48 and 72 hrs of age. Insect material was derived from field collected larvae and bred in the laboratory for one generation prior to experimentation. Adults were maintained under a daily regime of 14h light and 10h dark at a constant temperature of 25 °C. They were fed a 10 % honey solution as a nectar substitute. Oocyte morphology, the diameter of near terminal oocytes and the position of oocytes within the ovaries were recorded for 15 individuals of each species at each age using a dissecting microscope with an ocular micrometer. The presence or absence of conspicuous fat globules within the abdomens of individuals was recorded. For both *H. punctigera* and *H. armigera* at emergence, oocyte diameter was less than 0.25 mm, trophocytes (nurse cells) were present and oocytes were restricted to ovarioles. At 24 hours after emergence the oocyte diameter was 0.25 mm - 0.45 mm, and the oocytes had advanced to the apex of the calyx. At 48 hours and 72 hours from emergence the oocyte diameter was greater than 0.45 mm, and the oocytes had advanced to the lateral or common oviduct and the chorion was visibly ribbed.

Helicoverpa females were hence classed as immature if oocyte diameter was less than 0.45 mm, and oocytes were restricted to ovarioles and apex of the calyx. They were classed as mature if oocyte diameter was greater than 0.45 mm, and oocytes had advanced into the common oviduct and the chorion was visibly ribbed. The study was not intended to provide a detailed examination of the process of oogenesis in *H. punctigera* and *H. armigera.*

2.3 Results

In total, 366 *H. punctigera* and 132 *H. armigera* females were dissected during the study (Tables 2.1, 2.2). Most of the female moths of both species (89.9 % of *H. punctigera* and 88.7 % of *H . armigera*) were immature and unmated. There were no mated, immature females, but a single, unmated but mature *H. armigera* female was recorded (Table 2.1). In the case of *H. punctigera* , unmated, but mature females were recorded on two separate occasions (Table 2.2); the remaining females were mated and mature. A single catch of 229 *H. punctigera* females on the 28/12/89, accounted for 62.6 % of the total number females of that species examined. Immature females of both species had numerous globules of yellowish fat in the abdomen. These were not observed in mature females.

Most of the mated females contained only a single spermatophore (Table 2.3). Only 2.9 % of the mated *H. punctigera* females contained 2 spermatophores. Of the mated *H. armigera* females, 14.3% and 7.1% carried 2 and 3 spermatophores respectively.

2.4 Discussion

For both *H. punctigera* and *H. armigera* most females collected from the Point Lookout light trap were unmated and immature (they contained no fully developed eggs). Only a small proportion were mated or contained full sized eggs. In *Helicoverpa* spp. (Zalucki *et al.* 1986, this study) eggs are not developed at emergence. Egg development, however, proceeds following emergence and continues throughout the reproductive life of the female. Females commence oviposition once proximal eggs attain full size (> 0.45 mm) and have advanced to the common oviduct. In laboratory maintained adults this occurs within 1 - 3 nights after emergence for *H. armigera* and 1 - 5 nights for *H. punctigera* (see Chp. 3, Table 3.7) Given the above variability in time to first oviposition observed in both species it is not possible to assign a chronological age to the moths collected from the light trap based on their stage of reproductive development. Also, females collected from the light traps will have experienced varying temperature regimes and photoperiods. These factors are known to further influence the rate of egg development (McDonald & Cole 1991). In addition, laboratory reared moths are not subject to possible effects of prolonged flight activity, which is known to shorten the pre-reproductive period of noctuid moths (Willers *et al.* 1987). Females may, however, be classed as immature or mature based on their stage of reproductive development.

The onset of reproductive behaviour in Lepidoptera is manifested by the start of calling (pheromone release) in females, responsiveness of males to females, and mating (Engelmann 1970). There is, however, often a close relationship between the onset of calling and ovular maturation. For the cutworm, *Agrotis ipsilon,* Swier *et. al.* (1976) found that the proportion of females calling coincided closely with the degree of ovular maturation at a given age. Further, Kou & Chou (1987) reported that 70 % of *H. armigera* females commence calling within 3 nights of emergence. Though they did not directly relate the onset of calling with ovular maturity, there is a close similarity between the frequency distribution of age at first call reported in their study and age at first oviposition for *H. armigera* (see Chp 3. and Table 3.7). As *Helicoverpa* spp. commence oviposition once initial egg maturation has occurred, and this most likely coincides with the onset of calling, females can be classified as reproductively mature or immature based on the size and position of eggs in the ovaries. Though oviposition occurs whether moths are mated or not, presumably females are usually mated shortly after they reach reproductive maturity. As few *Helicoverpa* females collected from Point Lookout contained full sized eggs, and few were mated, they can be confidently classed as immature. Segregation of the catches into pre- and post-midnight fractions facilitated closer interpretation of the reproductive condition of migrant *H. punctigera* and *H. armigera.* Most catches occurred over one night and often over only half a night (Gregg et al. in press).

Few mated moths were encountered among either the *H. punctigera* or *H. armigera* females in light traps, suggesting that most mating takes place after migration. Also, the rarity of mature, but unmated females among *H. punctigera* and *H. armigera* moths, indicates that most females are probably mated by the time they are mature. Studies on *Heliothis virescens* have shown that mating frequency is positively correlated with age, indicating that single mating of moths is indicative of their recent emergence and maturation (Raulston *et al.* 1975). Of the mated *H. punctigera* and *H. armigera* females encountered, most contained only a single spermatophore.

The presence of conspicuous fat bodies in the moths trapped suggests that the duration of migratory flight prior to capture was insufficient to deplete reserves. Lipids have been identified as a major source of energy during flight (Van Handel 1974). Alternatively, sufficient fat is stored for flight and reproductive purposes. Presumably once reproductive maturity is reached and extensive flights are not undertaken, remaining fat reserves may be directed towards maximising reproductive effort. This is supported by the findings of Willers *et al.* (1987) who showed that a dichotomy existed in the identity of fuels used for flight and reproduction in *Heliothis virescens.* Prior to oviposition lipids are used as the primary flight fuel; however, once oviposition commences carbohydrates become increasingly important as flight fuel leaving lipids to be used for further reproductive development.

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Table 2.1 Numbers of females of *H. punctigera* trapped (by date) that were either mature or immature and mated or unmated. Numbers examined are also given as a proportion of the total catch of females on any one trap date.

Date	n	Prop. Total Catch	Number Mature Mated	Number Mature Unmated	Number Immature Mated	Number Immature Unmated
18-Nov-85	15	0.2	2	0	0	13
25-Nov-85	9	1.0	5	1	0	3
20-Jan-86	22	0.2	0	0	0	22
14-Dec-86	20	0.6	4	0	0	16
28-Dec-87	9	1.0	1	0	0	8
14-Mar-88	5	1.0	2	0	0	3
15-Mar-88	3	1.0	0	0	0	3
31-Jan-89	28	1.0	6	1	0	21
18-Nov-89	19	1.0	5	0	0	14
28-Dec-89	229	1.0	10	0	0	219
29-Dec-89	7	1.0	0	0	0	7
Total	366		35	2	0	329
%			9.6	0.5	0	89.9

Table 2.2 Numbers of females of *H. armigera* trapped (by date) that were either mature or immature and mated or unmated. Numbers examined are also given as a proportion of the total catch of females on any one trap date.

Date	n	Prop. Total Catch	Number Mature Mated	 Unmated	 Immature Mated	 Unmated
18-Nov-85	21	0.2	2	0	0	19
25-Nov-85	5	0.4	1	0	0	4
20-Jan-86	16	0.2	0	0	0	16
18-Mar-86	16	0.6	0	0	0	16
14-Dec-86	2	1.0	0	0	0	2
20-Dec-86	6	1.0	1	0	0	5
28-Dec-87	2	1.0	0	0	0	2
14-Mar-88	16	1.0	7	0	0	9
15-Mar-88	20	0.9	0	0	0	20
16-Mar-88	7	1.0	0	0	0	7
31-Jan-89	3	1.0	0	0	0	3
18-Nov-89	14	1.0	3	1	0	10
28-Dec-89	4	1.0	0	0	0	4
Total	132		14	1	0	117
%			10.6	0.7	0	88.7

Table 2.3 Percentage of mated *H. armigera* and *H. punctigera* females with one, two or three spermatophores. Data for all sampling dates were pooled.

		Number of Spermatophores		
	n	1	2	3
H. armigera	14	78.6	14.3	7.1
H. punctigera	35	97.1	2.9	-