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Migration and behavioral studies of two adult noctuid (Lepidoptera: Noctuidae) species plus feeding observations of some moths common to Iowa

William Hurston Hendrix III

Iowa State University

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Migration and behavioral studies of two adult noctuid (Lepidoptera: Noctuidae) species plus feeding observations of some moths common to Iowa

Hendrix, William Hurston, III, Ph.D.

Iowa State University, 1990
Migration and behavioral studies of two adult noctuid 
(Mothidae: Noctuidae) species plus feeding 
observations of some moths common to Iowa

by

William Hurston Hendrix, III

A Dissertation Submitted to the 
Graduate Faculty in Partial Fulfillment of the 
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Major: Entomology

Approved:

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For the Graduate College

Iowa State University
Ames, Iowa
1990
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INTRODUCTION

Many North American crops are regularly attacked by large numbers of economically important noctuid (Lepidoptera: Noctuidae) species. These insects are known to be highly mobile (see McNeil 1987), expanding their breeding range far beyond their overwintering areas. In Iowa, two of the most important noctuids are the armyworm, *Pseudaletia unipuncta* (Haworth) and the black cutworm, *Agrotis ipsilon* (Hufnagel). Both species cause sporadic economic damage to corn and are thought to be migratory in nature (e.g., McNeil 1987, Showers et al. 1989b).

Eclosion periodicity can be related to the migratory potential of the black cutworm and armyworm. Daily eclosion is important in understanding the activity of moths and their availability for flight. The moths could emerge during the day and presumably remain inactive until the next night. Conversely, the moths might emerge early in the evening and be able to feed or fly the first evening. In a laboratory colony of black cutworm, emergence was found to peak at 2200 hr (Nasr and Naguib 1963). The effect of long-term rearing and the effect of cold storage, however, has not been examined. To maintain a colony and provide sufficient numbers of insects for a large-scale adult mark-release-recapture program, moths must routinely be kept in cold storage. Although laboratory colonies are normally replaced each year to maintain genetic vigor, rearing mishaps can occur, prohibiting the maintaining and expansion of these new colonies. The effects of cold storage and colony
age, therefore, would be of concern if these two conditions disrupted daily eclosion of moths.

Feeding behavior of newly emerged moths can provide information on ovipositional and migratory ability of moths. If a female is provided a nectar meal, she can produce more eggs (Nuttycombe 1930). The European corn borer, *Ostrinia nubilalis* (Hübner), maintains egg weights if fed a honey-water solution (Miller 1988). An adult food source can also provide energy for newly emerged moths.

One of the least studied behaviors is feeding of moths in the field. Several large treatises have been published (e.g., Robertson 1929, Nuttycombe 1930, Brantjes and Leemans 1976). Most records, however, are widely scattered in the literature and none could be found concerning feeding in Iowa.

Although migration is thought to play a part in the insect's population dynamics, little empirical evidence has been provided concerning their movement. Showers et al. (1989a) and Showers et al. (1989b) provided such evidence with mark-release-recapture studies of black cutworm. Movement was recorded from release sites in Texas and Louisiana to trap locations in Missouri, Kansas, and Iowa. The long-range dispersal was tracked using wind trajectory analysis, providing direct evidence for meteorologically driven migration. Direct evidence for migration was provided in another manner (Hendrix et al. 1987). The authors examined Arkansas collected corn earworm, *Heliothis zea* (Boddie), for pollen. By identifying exotic pollens and back-tracking the location of these pollens, evidence was provided for long-distance movement in
this species. This method, however, has not been used for the black cutworm or the armyworm. Successful use of this technique would provide empirical information concerning the migratory ability of the armyworm and confirm Showers et al. (1989a, 1989b) findings with the black cutworm. Further, it would help elucidate the site of origin of these naturally marked immigrants.

The objectives of this study are fourfold. The first is to examine the eclosion periodicity in both the daily emergence rhythms and the population cycle and the impact of cold storage and long-term laboratory rearing on these parameters. The second objective is to examine the posteclosion feeding of adult armyworm and black cutworm to elucidate the timing posteclosion of this feeding. The third objective is to collect information on adult moth feeding on common Iowa plants throughout the season. The final objective of this research is to determine if pollen analysis can be used to trace the long-distance migration of the black cutworm and armyworm. Such evidence would provide critical details of the overwintering sites and provide the first direct evidence for long-distance migration of armyworm. In total, this research provides needed information of important adult behavior for two Iowa pest species.
LITERATURE REVIEW

Noctuid Adult Eclosion

Time of emergence is critical for all insects. Daily rhythms are found in most species. These rhythms synchronize the individual to the population. Often discrete windows of emergence are observed and few pupae emerge outside this window. Records are scarce for this type of behavior, and even more so for the effects laboratory conditions have on the population.

It has been recorded, however, that many butterflies and sphingid moths emerge in the morning while most noctuids emerge in the evening (Bremer 1926, in Scott 1936). The effects of different temperatures, barometric pressures, humidities and scotophases on the Mediterranean flour moth, Anagasta kuehniella (Zeller), have been studied as well (Scott 1936). Barometric pressure and humidity were not found to have an effect on emergence rhythm. Temperature, however, had a strong effect. As the temperature fell, there was a corresponding period of maximum emergence of moths. When temperatures were held constant, a rhythm continued to be noticeable. The rhythm was present after three generations at constant conditions. These results suggest emergence rhythms must be inherited. Dreisig (1986) also provides a review of current literature on emergence times. He concluded that most nocturnal moths emerge in the afternoon and/or early evening. Most of the reviewed nocturnal insects mated the first night after emergence.
The female often begins calling soon after emergence while the male emerges first because of sexual competition. Conversely, in a number of species, the females do not start calling until several days after eclosion and male emergence commonly occurs at the same time as the female. These species might have a different pattern of emergence. The armyworm does not call on the day following emergence but generally begins to call several days after emergence (Turgeon and McNeil 1982, 1983). Only 20% of black cutworm females began to call after 1 d; 4-day-old females call the most frequently. This behavior corresponded to sexual maturity of the moth (Swier et al. 1977).

Maximum adult emergence of sod webworm, *Cramibus trisectus* (Walker), occurred between 2100 and 0100 hr (Banerjee and Decker 1966). The males emerged earlier and were predominant during the first few hours. Mating began on the night of emergence. The emergence of red hairy caterpillar, *Amsacta moorei* (Butler), and castor hairy caterpillar, *Euproctis lunata* (Walker) has also been studied (Singh 1972). Emergence of *A. moorei* was confined to the later part of the day. The maximum emergence occurred from 1200 to 1730 hr. None emerged after sunset and no differences were found between the sexes. *E. lunata* peak emergence was between 1230 and 1800 hr. Again, differences were not found between the sexes.

Emergence of *Halisidota argentata* (Pack.), a defoliator, was closely associated with exposure of late instar and pupae to sunset times. There was no difference between the sexes. In the laboratory, emergence was from sunset, 1900 hr to 2100 hr. If pupae were placed in constant dark, the emergence interval was primarily 1600-2200 hr (Edwards 1964).
With the moth, *Ephestia kuhniella* (Zell.), variations of light, independent of any associated temperature variations, can cause changes in the emergence rhythm (Moriarty 1959). Emergence was not dependent on light conditions during the earlier stages of larval development. The later stages of development were synchronized with a biological clock regulated within the brain. If the pupae are exposed to light during this period, the clock stops and the cycle can only be set in motion again after the light is removed (Giebultowicz and Cymborowski 1976).

Emergence of the lesser peachtree borer, *Synanthedon pictipes* (Grote and Robinson) occurred during the morning hours and, at times, was related to temperature conditions (Gorsuch and Karandinos 1974). A certain number of thermal units must be accumulated following sunrise for emergence to take place. The ratio of males declined significantly on both daily and seasonal scales.

Experimentation with the pink bollworm, *Pectinophora gossypiella* (Saunders), indicated moth emergence in the laboratory or the field occurred between 0700 and 1000 hr (Lingren 1983). Smaller peaks occurred from 1400 to 1700 hr and from 1800 to 2100 hr. Male and female moth emergence occurred throughout the day, but a peak occurred from 0800 and 1000 hr. Female moth emergence was initiated before male emergence (Henneberry and Clayton 1986).

A specially constructed emergence counter was used to study the gypsy moth, *Lymantria dispar* (L.) (Ma et al. 1982). This counter triggered an event recorder as the moth pushed its way out of an artificial pupal chamber. Emergence occurred within 10 hr after the onset of light with a
photoperiod of 16:8 LD. Peak eclosion time for males was 3.14 hr after
lights on, while females peaked at 5.34 hr. Eclosion was specific for a
time of day and if developing adults were not at the correct development
stage or "gate", they remained in the pupal skin until the following day.

Eclosion has been observed in several species of noctuids. Female
Heliothis armigera (Hübner), in the Sudan Gezira, emerged about one hour
earlier (1832 hr) than males (1929 hr) (Topper 1987). Emergence of
Spodoptera exempta (Wlk.) in the field occurred from 1900 to 2230 hr
(Topper 1987). Emergence of greenhouse-reared cabbage loopers,
Trichoplusia ni (Hübner), occurred primarily during the daylight hours
with a majority occurring in the morning (Shorey et al. 1962).

Light trap captures of corn earworm, Heliotris zeae (Boddie), showed
that during the first week of each generation there were twice as many
males as females (Gaines 1933). When examining hourly emergence, of 52
emergent moths observed in one study, 30 emerged during the day and 22 at
night (Garman and Jewett 1914). In a direct contradiction, other studies
found that laboratory reared corn earworm emergence occurred primarily
during night and very early morning (Quaintance and Brues 1905, Hardwick
1965). In addition, 94.6% of the emergence occurred between 1900 and
2300 hr, with 38.2% emerging between 2100 and 2200 hr (Callahan 1958).
None emerged after midnight. The peak eclosion times seemed to coincide
with peak activity times of the moth (Hardwick 1965). When examining
field populations of corn earworm, emergence begins from 2000 to 2200 hr,
peaking from 2100 to 2300 hr (Lingren et al. 1988). Eclosion ceased
between 2400 and 0200 hr. Females were more common during the early stages of the emergence cycle.

Little information could be gathered concerning armyworm emergence. Hundreds of armyworms were observed emerging after a rain shower (Knight 1916). Further, Knight (1916) stated "the sunshine seemed to produce exactly the right condition to bring forth the moths...each evening those moths that emerged during the day flew away in all directions, probably in search of food and for mating".

In a laboratory colony of pale western cutworm, *Agrotis orthogonia* (Morrison), 90.7% of both sexes emerged between noon and midnight, with nearly half emerging between 1400 and 1600 hr (Jacobson 1965). In a laboratory colony, 93% of black cutworm, *Agrotis ipsilon* (Hufnagel), emergence occurred between sunset and sunrise (Nasr and Naguib 1963). Most emerged between 2000 and 0400 hr with a peak at 2200 hr.

**Feeding Behavior**

**Feeding studies in the field**

Once the adult has emerged, a food source is often required. This food source, frequently nectar, provides energy for flight and reproduction. The feeding behavior of newly emerged moths can provide information on the ovipositional and migratory ability of the moths and the timing of these important behaviors.

Early researchers made field observations of nocturnal feeding to better understand a pest species. Because it had little impact on
control, this practice was largely discontinued after the advent of large-scale insecticide usage. With the development of pheromones and an increase in environmental concerns, more attention has been paid to the nocturnal behavior of moths, including feeding. Additional information concerning the behavior of noctuids should help in the development of more efficient means for attracting, trapping and manipulating adult moths (Lingren et al. 1977).

A general understanding of pollination syndromes, and the behaviors of Lepidoptera associated with them, provides a general introduction to moth feeding. Botanists generally divide Lepidoptera pollination activity into two types: the moth and the butterfly flowers. Butterfly flowers differ from most moth flowers by being attractive during the day. In general, butterflies tend to favor composites and other flowers with small tubular flowers grouped together (Proctor and Yeo 1973). Flower color is chiefly blue and deep pink and, in the tropics, scarlet. The butterflies visit flowers with flat-topped corollas or other landing platforms (Percival 1965). These insects have good color sense as well as excellent odor perception. Nectar from these flowers is classified as being spicier than nectar from moth flowers. However, butterflies may be more attracted to a plant by visual cues than olfactory cues (Percival 1965). Nectar flow from these plants is fairly copious and occurs during the day. The nectar is either sucrose-rich, i.e., butterfly bush, *Buddleja davidii*, or hexose-rich as is common in most composites (Baker and Baker 1983).
Moth flowers, usually pale in color, are characterized by having a heavy, sweet scent. Most have well developed colors not visible to the human eye (Meeuse 1961). Many have long narrow corolla tubes and their petal lobes stand at right angles to the ground. They often present a flat face so that no lip or landing platform is available for the insect. Nectar flow is nocturnal and is sucrose-rich or sucrose dominant (Baker and Baker 1983). Moths often find flowers by approaching upwind using an odor trail similar to that used by moths when attracted to sexual pheromones. Many flowers have both visual and olfactory nectar-guides. An abundance of nectar is usually provided.

The moth-pollinated flowers might be further divided into those visited by hawk moths (Sphingidae) and those visited by other moths (especially noctuids and geometrids). The hawk moth flowers are typified by honeysuckle, four o'clocks and jimson weed. The corolla tube is longer than those found in other moth-pollinated flowers and the hawk moths will not alight while visiting the flower. Sphingid moths often use the nectar guides while the noctuids direct the proboscis with the aid of differences in odor quality (Brantjes 1978). Most moths are "settlers", alighting but fluttering their wings.

The daily onset of nocturnal flight is very important in synchronizing the insect with the plant's nectar flow. The timing of daily activities is thought to be controlled by factors at three levels: a.) ecological factors which restrict the activities of an insect species to the most optimal time; b.) proximate factors that act as signals especially for daily rhythms; c.) an endogenous process called
circadian rhythm (Dreisig 1986). Onset of nightly activity is not an immediate, kinetic response to a decrease in light intensity. Activity occurs after a physiological preparatory process (latency period) involving transition from an inhibiting to an uninhibiting output of the central nervous center (Dreisig 1978). In the cabbage looper, the light intensity registered by the ocelli determines the threshold for flight (Eaton et al. 1983). Further, different species commence activity at different light intensities and, within a given species, the longer the twilight the greater the disparity of activity onset (Dreisig 1980).

Light traps can provide valuable information about the flight activity of insects. However, light traps are not attractive to all species or even consistently for the same species. Insect activity, measured by light traps in Mississippi, showed that the majority of noctuids were captured between 0100 and 0500 hr (Hutchins 1940). However, the percentage of male noctuids increased throughout the night. Capture did not seem to be correlated with temperature until the temperature dropped below 6°C. In Brownsville, Texas, light trap captures for H. zea, H. virescens (Fabr.), T. ni, Estigmene acraea (Drury), Pectinophora gossypiella (Saunders) and Alabama argillacea (Hübner) were examined for activity patterns (Graham et al. 1964). H. zea, H. virescens and T. ni, had similar flight activity with peaks between 0130 and 0330 hr, with little differences between the sexes. Alabama argillacea was different from the other noctuids, producing a distinct flight pattern between sexes. Females increased gradually, peaked at 0130 to 0330 hr, then declined. The males showed a similar
increase and peak, but did not decline. The arctiid, *E. acraea*, was collected earlier in the night. Males showed a strong peak near 2130 hr and females peaked at 2330 hr. The gelichiid, *P. gossypiella*, peaked in the early evening for both sexes, but the males showed a second peak at 0130 hr, while the females declined steadily. These results for *P. gossypiella* agreed with those from Egypt (Ballou 1920) and from Hawaii (Busk 1917), but were in conflict with results from Texas (Glick et al. 1956) and from Algeria (Delassus 1931). Most notable was a study in India, showing a peak occurred during the last 4 hr of night early in the cotton (*Gossypium hirsutum* L.) season, the middle 4 hr in mid-season, and the first 4 hr at the end of the season (Hussain et al. 1934). The maximum activity of tobacco hornworm moths, *Manduca sexta* (Johannson), was 2100 to 2200 hr for males with a steady decline after 2200 hr (Stewart et al. 1967). Females were similar to males except activity was reduced between 2000 and 2100 hr. In the same study, corn earworm moth activity increased until 0100 hr, whereupon a sharp decline was recorded.

Activity patterns of pyralids has also been studied. Females of the pyralid, *Crambus teterrellus*, appeared very shortly after dusk, whereas comparatively few males came until later in the evening (Ainslie 1917). The males reached a peak between 2330 and 0130 hr. European corn borer, *Ostrinia nubilalis* (Hübner), was shown to have a bimodal flight pattern upon examination of blacklight trap catches (Huber et al. 1928). The first flight began shortly after dusk. The early evening flight was stimulated by environmental or endogenous factors other than mate-seeking. However, egg deposition occurred during this flight. Sexual
activity, as shown by capture in sex pheromone traps, peaked between 2400 and 0100 hr (Showers et al. 1976).

Moon phase has long been thought by entomologists to have an influence on moth activity. However, conflicting results are found in the literature regarding moon phases. Noctuid moth activity seems to be influenced by temperature but not by lunar phase in western North America (Hardwick 1972). In England, it was noted moonlight did affect the activity of nocturnal insects (Williams 1936, Williams and Singh 1951). New evidence reversed the earlier findings, however, and it was concluded the effect of moonlight could not be demonstrated (Williams et al. 1956). A study of corn earworm activity at light traps for three consecutive years discovered a rhythmic pattern corresponding to the lunar phases (Nemec 1971). More moths were captured during the new moon than during the full moon. Numbers of corn earworm eggs also fluctuated with relation to moon phases. It was concluded, therefore, that corn earworm generation cycles are synchronized or governed by lunar phases (Nemec 1971). Further, in another study, the lowest numbers of corn earworms were always collected during the full moon (Agee et al. 1972). Even when the full moon nights were cloudy and overcast, the collections of moths were low. These results agree with findings from Georgia with corn earworm (Beckham 1970), but conflict with results from Egypt on black cutworm capture (Hanna and Atries 1969). At least one researcher has shown that the moon did not have a direct effect but reduced collections because of the reduced attraction of the artificial light source (Dufay 1964).
Vibration sensitive actographs can also record moth activity in the laboratory. When examined with such a recorder, cabbage looper moths were shown to have age-related activity patterns during a scotophase of 2000 to 0600 hr (Leppla et al. 1979). During the first eight days, both sexes were active through the scotophase. In this same study, soybean loopers and fall armyworm males were significantly more active than females of the species. Velvetbean caterpillar, *Anticarsia gemmatalis* (Hübner), females were more active than the males. Corn earworm sexes were equivalent. When using the actograph to study corn earworm activity in relation to temperature, low temperatures (10 to 15.6°C) caused activity during the first 6 hours following nightfall (Hsiao 1978). At higher temperatures, the activity increased and lasted longer. However, activity for mating or feeding can not be distinguished using an actograph and is a severe limiting factor in its usefulness for feeding studies.

One of the most useful, if old fashioned, methods of recording feeding activity is simple observation. One of the most extensive articles on the feeding habits of moths reports on feeding activity from nectar, water, sap, honeydew and animal excreta (Norris 1936). The noctuid moths comprised a larger proportion of nectar feeders than did the geometrids. Further, the Sphingidae are notable nectar feeders and were often observed because of their large size.

In California, three sphingid species, *Celerio lineata*, *Pholus achemon* and *Phlegethontius sexta*, were most commonly found pollinating the genus *Oenothera*, the evening primrose (Gregory 1964). Sphingids have
strong flight ability and are able to range widely while feeding. *Mirabilis* spp. (Nyctaginaceae) were visited by the hawk moths *Sphinx chersis* (Hübner) and *Pholus achemon* (Drury) (Cruden 1970). The hawk moths began to visit at 1945 hr (MST), as soon as the flower was receptive and produced an odor. Pollen found on one hawk moth offered proof of pollination. Finally, hawk moths were observed pollinating and carrying pollen from two lilies in the Netherlands (Brantjes and Bos 1980).

In America, one of the most extensive feeding lists was compiled from observations in Illinois (Robertson 1929). For brevity, the results for noctuids, geometrids, pyralids and sphingids are presented in Table 1. Other feeding references, however, are varied and widely dispersed throughout the literature.

The noctuid, *Hadena biruris* (Hufnagel), was observed feeding on *Melandrium album* (Mill.) (Brantjes 1976). A list of visitors to *Silene otites* (L.) growing in the Netherlands has also been compiled (Brantjes and Leemans 1976) (Table 2). Twenty species of Plusiinae (Noctuidae), including *Autographa precationis* (Gn.), were recorded from hosts in northern Michigan (Nielsen 1981). The host plants collected from were *Asclepias syriaca* (L.), *Apocynum androsaemifolium* (L.), *Centaurea maculosa* (Lam.), *Epilobium angustifolium* (L.), *Cirsium* sp., *Diervilla lonicera* (L.), and *Eupatorium* sp. Extensive tests on *Autographa gamma*, both in the laboratory and in the field found the first moths always appeared at dusk and flight activity began earlier in the evening as
Table 1. Feeding records of large nocturnal moths as recorded by Robertson (1929)

<table>
<thead>
<tr>
<th>Insect</th>
<th>Family</th>
<th>Plant</th>
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<tr>
<td><strong>Arctiidae</strong></td>
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<tr>
<td><em>Callimorpha fulvicosta</em> (Clm.)</td>
<td>Asclepiadaceae</td>
<td><em>Asclepias syriaca</em></td>
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<tr>
<td><em>Utetheisa bella</em> (L.)</td>
<td>Compositae</td>
<td><em>Boltonia asteroides</em></td>
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<td>&quot;</td>
<td>Compositae</td>
<td><em>Solidago graminifolia</em></td>
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<tr>
<td>&quot;</td>
<td>Compositae</td>
<td><em>Solidago nemoralis</em></td>
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<tr>
<td><strong>Noctuidae</strong></td>
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<tr>
<td><em>Acontia candefacta</em> (Hübner)</td>
<td>Umbelliferae</td>
<td><em>Eryngium yuccifolium</em></td>
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<tr>
<td><em>Alypia octomaculata</em> (F.)</td>
<td>Rutaceae</td>
<td><em>Ptelea trifoliata</em></td>
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<tr>
<td><em>Agrotis ipsilon</em> (Hufnagel)</td>
<td>Asclepiadaceae</td>
<td><em>Asclepias syriaca</em></td>
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<tr>
<td><em>Autographa precationis</em> (Gn.)</td>
<td>Labiatae</td>
<td><em>Stachys palustris</em></td>
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<tr>
<td><em>Caenurgina erechtea</em> (Cramer)</td>
<td>Asclepiadaceae</td>
<td><em>Asclepias syriaca</em></td>
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<tr>
<td><em>Feltia ducens</em> (Walker)</td>
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<td>Psoralea onobrychis</td>
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<td>Lithospermum canescens</td>
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<td>Aster novaengliae</td>
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<td>Rudbeckia hirta</td>
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<td>Labiatae</td>
<td>Nepeta hederacea</td>
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<td>Leguminosae</td>
<td>Trifolium pratense</td>
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Table 1. continued

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<thead>
<tr>
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<td>Phlox pilosa</td>
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<td>Rosaceae</td>
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<td>Asclepias syriaca</td>
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<td>Antennaria plantaginifolia</td>
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<td>&quot;</td>
<td>Scrophulariaceae</td>
<td>Veronica virginica</td>
</tr>
<tr>
<td>Nompohila noctuella (Voll.)</td>
<td>Scrophulariaceae</td>
<td>Veronica virginica</td>
</tr>
</tbody>
</table>

**Sphingidae**

| Chaerocampa tersa (L.) | Asclepiadaceae | Asclepias syriaca |
| "                   | Orchidaceae | Habenaria leucophaea |
| Hyles lineata (F.) | Boranginaceae | Mertensia virginica |
| "                   | Compositae | Cirsium altissimum |
| "                   | Compositae | Cirsium discolor |
Table 1. continued

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>Genus</th>
</tr>
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<tbody>
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<td>Hyles lineata (F.)</td>
<td>Convolvulaceae</td>
<td>Ipomoea purpurea</td>
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<td>Leguminosae</td>
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<td>&quot;</td>
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<td>&quot;</td>
<td>Ranunculaceae</td>
<td>Delphinium tricolor</td>
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<td>Scrophulariaceae</td>
<td>Pentstemon laevigatus</td>
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<td>Datura tatula</td>
</tr>
<tr>
<td>Hemaris axillaris (G. &amp; R.)</td>
<td>Asclepiadaceae</td>
<td>Asclepias sullivantii</td>
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</tr>
<tr>
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<td>Labiatae</td>
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</tr>
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<td>Leguminosae</td>
<td>Trifolium pratense</td>
</tr>
<tr>
<td>&quot;</td>
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<td>Verbena stricta</td>
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<tr>
<td>Hemaris thysbe (F.)</td>
<td>Boranginaceae</td>
<td>Mertensia virginica</td>
</tr>
<tr>
<td>&quot;</td>
<td>Caprifoliaceae</td>
<td>Viburnum prunifolium</td>
</tr>
<tr>
<td>&quot;</td>
<td>Compositae</td>
<td>Cirsium altissimum</td>
</tr>
<tr>
<td>&quot;</td>
<td>Compositae</td>
<td>Cirsium discolor</td>
</tr>
<tr>
<td>&quot;</td>
<td>Geraniaceae</td>
<td>Geranium maculatum</td>
</tr>
<tr>
<td>&quot;</td>
<td>Labiatae</td>
<td>Monarda fistulosa</td>
</tr>
<tr>
<td>&quot;</td>
<td>Leguminosae</td>
<td>Psoralea oblongifolium</td>
</tr>
<tr>
<td>&quot;</td>
<td>Polemoniaceae</td>
<td>Phlox divaricata</td>
</tr>
<tr>
<td>&quot;</td>
<td>Polemoniaceae</td>
<td>Polemonium reptans</td>
</tr>
<tr>
<td>Philampelus pandorus (Hübner)</td>
<td>Solanaceae</td>
<td>Datura stramonium</td>
</tr>
<tr>
<td>Protoparce celeus (Hübner)</td>
<td>Solanaceae</td>
<td>Datura stramonium</td>
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<tr>
<td>Species</td>
<td>Family</td>
<td>Plant Name</td>
</tr>
<tr>
<td>-------------------------</td>
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<td>--------------</td>
</tr>
<tr>
<td><em>Protoparce celeus</em> (Hübner)</td>
<td>Solanaceae</td>
<td><em>Datura tatula</em></td>
</tr>
<tr>
<td><em>Sphinx eremitus</em> (Hübner)</td>
<td>Convolvulaceae</td>
<td><em>Ipomoea pandurata</em></td>
</tr>
</tbody>
</table>
the season progressed (Schremmer 1941). Moths were seen on *Scabiosa ochroleuca*, *Melandryum album*, *Silene vulgaris*, *Dianthus sp.* and *Trifolium sp.*

Several cotton insects have been studied at night. Cabbage loopers were observed feeding on spiny aster, *Aster spinosus* (Benth.), in California (Shorey et al. 1962). The moths also fed actively from blossoms and nectaries of cotton. Moth activity began about 30 min before sunset, and then increased. In studies with the tobacco budworm, adults began feeding between 1900 and 2000 hr, (AST) but peak feeding activity for females occurred about 1 hr later than that of males (Lingren et al. 1979). Feeding activity was observed in Puerto Rico and St. Croix until 0300 to 0400 hr on pigeonpea and *Bastardia* sp. Both the cabbage looper and soybean looper, *Pseudoplusia includens* (Walker), were observed to be active in large numbers in cotton and soybean fields in Alabama while *Syngrapha u-aureum* were readily taken from goldenrod, *Solidago* spp. (Eichlin and Cunningham 1978).

Many *Alabama argillacea* and *Heliothis armigera* were found to feed on the extrafloral nectaries of cotton (Butler et al. 1972). Similarly, soybean looper were observed feeding on cotton nectar (Jensen et al. 1974). The cotton leaf perforator, *Buccalatrix thurberiella* (Busck.), fed extensively on both square and leaf nectaries (Lingren et al. 1980). Activity began near dusk, peaked shortly thereafter, and decreased during the rest of the night. The tobacco budworm, *Heliothis virescens*, and cabbage looper fed on tobacco and careless weed, *Amaranthus spinosus* (Lingren et al. 1977). Both began their activity at 2000 hr.
Table 2. Insects attracted to *Silene otites* (Caryophyllaceae) as reported by Brantjes and Leemans (1976)

<table>
<thead>
<tr>
<th>Insect</th>
<th>Insect</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Geometridae</strong></td>
<td><strong>Noctuidae</strong></td>
</tr>
<tr>
<td><em>Cyclophora linearia</em> (Hübner)</td>
<td><em>Euxoa obelisca</em> (Schiff.)</td>
</tr>
<tr>
<td><em>Idaea seriata</em> (Schrank)</td>
<td><em>Scotia segetum</em> (Schiff.)</td>
</tr>
<tr>
<td><em>I. aversata</em> (L.)</td>
<td><em>Ochropiura plecta</em> (L.)</td>
</tr>
<tr>
<td><em>Xanthorhoe spadicearia</em> (D. &amp; S.)</td>
<td><em>Noctua pronuba</em> (L.)</td>
</tr>
<tr>
<td><em>X. designata</em> (Hufnagel)</td>
<td>*Dicestra trifoli (Hufnagel)</td>
</tr>
<tr>
<td><em>X. ferrugata</em> (Clerck)</td>
<td><em>Hamestra brassicae</em> (L.)</td>
</tr>
<tr>
<td><em>X. fluctuata</em> (L.)</td>
<td><em>Hadena rivularis</em> (Fabr.)</td>
</tr>
<tr>
<td><em>Epirohoe alternata</em> (Muller)</td>
<td><em>Mesapamea secalis</em> (L.)</td>
</tr>
<tr>
<td><em>Camptogranus bilineatus</em> (L.)</td>
<td><em>Mesoligia furunculata</em> (Schiff.)</td>
</tr>
<tr>
<td><em>Cosmorhoe ocellata</em> (L.)</td>
<td><em>Phlogophora meticulosa</em> (L.)</td>
</tr>
<tr>
<td><em>Chloroclysta truncata</em> (Hufnagel)</td>
<td><em>Caradrina clavipalpis</em> (Scop.)</td>
</tr>
<tr>
<td><em>Thera obelisca</em> (Hübner)</td>
<td><em>Cosmia trapezina</em> (L.)</td>
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<tr>
<td><em>Perizoma alchemillata</em> (L.)</td>
<td><em>Autographa gamma</em> (L.)</td>
</tr>
<tr>
<td><em>P. flavofasciata</em> (Thunberg)</td>
<td><em>Plusia chrysitis</em> (L.)</td>
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<tr>
<td><em>Eupithecia centaureata</em> (D. &amp; S.)</td>
<td><em>Rivula sericealis</em> (Scop.)</td>
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<td><em>E. goossensiata</em> (Mabille)</td>
<td><em>Hypaena proboscidalis</em> (L.)</td>
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<tr>
<td><em>E. icterata</em> (Villers)</td>
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<td><em>E. succenturiata</em> (L.)</td>
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<tr>
<td><em>Gymnoscelis rufifasciata</em> (Haworth)</td>
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<td><em>Apocera efformata</em> (Guenee)</td>
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<td><em>Semiothisa notata</em> (L.)</td>
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<td><em>S. liturata</em> (Clerck)</td>
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<td><em>Opistograptis lutcolata</em> (L.)</td>
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<td><em>Epione repandaria</em> (Hufnagel)</td>
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<tr>
<td><em>Campaea margaritata</em> (L.)</td>
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</tr>
<tr>
<td><em>Lithosia complana</em> (L.)</td>
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</tr>
</tbody>
</table>
*Heliothis armigera* fed on cotton and tassel-stage sorghum (Topper 1987). Where food was scarce, activity began at 1815 hr (GMT + 2 hr) and peaked between 1815 and 1930 hr. After 1930 hr, activity decreased almost linearly. Flight activity where food was plentiful started to decline earlier and more quickly.

The corn earworm, because of its economic importance, has been studied more extensively. Large numbers of corn earworm were attracted to blooming soybean (*Glycine max* L.) fields (Barber 1938). An extensive feeding list of attractive plants for the corn earworm has been compiled from both captive studies and from nature (Table 3) (Nuttycombe 1930). From this same study, food was found to be a strong factor in determining the number of eggs deposited by corn earworm females. Females were able to produce a large complement of eggs on several plants of interest. Listed by importance for egg-laying they were: alfalfa, *Medicago sativa* (L.); red clover, *Trifolium pratense* (L.); milkweed, *Asclepias* sp.; and white clover, *Trifolium repens* (L.). The females presented goldenrod did not produce any eggs. Corn earworm was also observed feeding on cotton, Joepye weed (*Eupatorium purpureum* L.), plum (*Prunus americana* Marsh.), sunflower (*Helianthus* sp.) and buffalo bur (*Solanum rostratum* Dunal) (Quaintance and Brues 1905). Feeding usually began after 1800 or 1900 hr, but if food was scarce feeding began earlier. Further, feeding on sweet clover, *Melilotus alba* (Desr.), (Garman and Jewett 1914), and lima bean, *Phaseolus limensis* (L.), (Pepper 1943) have been reported. Feeding on tobacco, *Nicotiana tabacum* (L.); bush bean, *Phaseolus vulgaris* (L.); Petunia, *Petunia* spp.; hog peanut,
Table 3. Attractive plants to the corn earworm, *Heliothis zea* from Nuttycombe (1930)

<table>
<thead>
<tr>
<th>Family</th>
<th>Plant</th>
<th>Common Name</th>
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</thead>
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<td>Anacardiaceae</td>
<td><em>Rhus</em> sp.</td>
<td>Sumac</td>
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<tr>
<td>Apocynaceae</td>
<td><em>Apocynum cannabinum</em> L.</td>
<td>Indian hemp</td>
</tr>
<tr>
<td>Asclepiadaceae</td>
<td><em>Asclepias syriaca</em> L.</td>
<td>Common milkweed</td>
</tr>
<tr>
<td>Compositae</td>
<td><em>Achillea millefolium</em> L.</td>
<td>Milfoil</td>
</tr>
<tr>
<td>Compositae</td>
<td><em>Anthemis cotula</em> L.</td>
<td>Dog-fennel</td>
</tr>
<tr>
<td>Compositae</td>
<td><em>Aster</em> sp.</td>
<td>Wild aster</td>
</tr>
<tr>
<td>Compositae</td>
<td><em>Chrysanthemum</em> spp.</td>
<td>Daisy</td>
</tr>
<tr>
<td>Compositae</td>
<td><em>Erigeron</em> sp.</td>
<td>Erigeron</td>
</tr>
<tr>
<td>Compositae</td>
<td><em>Eupatorium purpureum</em> L.</td>
<td>Joepey weed</td>
</tr>
<tr>
<td>Compositae</td>
<td><em>Rudbeckia</em> sp.</td>
<td>Cone-flower</td>
</tr>
<tr>
<td>Labiatae</td>
<td><em>Nepeta cataria</em> L.</td>
<td>Catnip</td>
</tr>
<tr>
<td>Leguminosae</td>
<td><em>Medicago sativa</em> L.</td>
<td>Alfalfa</td>
</tr>
<tr>
<td>Leguminosae</td>
<td><em>Trifolium agrarium</em> L.</td>
<td>Hop clover</td>
</tr>
<tr>
<td>Leguminosae</td>
<td><em>Trifolium arvense</em> L.</td>
<td>Rabbit-foot clover</td>
</tr>
<tr>
<td>Leguminosae</td>
<td><em>Trifolium pratense</em> L.</td>
<td>Red clover</td>
</tr>
<tr>
<td>Leguminosae</td>
<td><em>Trifolium repens</em> L.</td>
<td>White clover</td>
</tr>
<tr>
<td>Leguminosae</td>
<td><em>Vicia</em> sp.</td>
<td>Wild vetch</td>
</tr>
<tr>
<td>Leguminosae</td>
<td><em>Vigna sinensis</em> L.</td>
<td>Cowpea</td>
</tr>
<tr>
<td>Liliaceae</td>
<td><em>Allium vineale</em> L.</td>
<td>Wild onion</td>
</tr>
<tr>
<td>Rubiaceae</td>
<td><em>Cephalanthus occidentalis</em> L.</td>
<td>Button-bush</td>
</tr>
<tr>
<td>Solanaceae</td>
<td><em>Solanum carolinense</em> L.</td>
<td>Horse nettle</td>
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<tr>
<td>Umbelliferae</td>
<td><em>Daucus carota</em> L.</td>
<td>Wild carrot</td>
</tr>
</tbody>
</table>
Amphicarpa bracteata (L.); jimson weed, Datura stramonium (L.); morning glory, Ipomoea purpurea (L.); and puncture vine, Tribulus terrestris (L.) were reported in a separate study (Callahan 1958). Feeding on pigeonpea (Cajanus cajan) nectar was noted to be heaviest before and during sunset (Adler 1987).

The corn earworm was observed extensively in Arkansas (Phillips and Whitcomb 1962). Feeding usually began between 1630 and 1700 hr (CST). The moths were observed to feed on crimson clover, white clover, sweet clover, alfalfa, evening primrose, and cotton. The only feeding observed in corn was that on honeydew secreted by aphids. Further, two species of grass, rye-grass, Lolium perenne L., and Dallis grass, Paspalum dilatatum Poir., were attractive because of the exudate produced by Claviceps purpurea (Fr.). In Botswana, corn earworm feeding on sorghum and corn began with moth activity at dusk and decreased until 2400 hr (Roome 1975). In another study, corn earworm moth activity began just at dusk and ceased at daylight in Texas, with the moths visiting a large number of cotton plants during this time (Gaines 1933). Corn earworm moths were reported active on the nectaries of the cotton plant in Texas (Fletcher 1929). Newly emerged corn earworm moths were observed feeding on corn exudates before their wings were even expanded (between 11 and 69 min after emergence) (Lingren et al. 1988). The corn earworm moth has also been observed feeding on a number of wild flowers growing along the Rio Grande in Texas (Raulston et al., in review). These flowers were Gaura odorata (Lag.), Helianthus spp., Clematis drummondii (T. & G.) and on the seed heads of buffelgrass, Cenchrus ciliaris (L.). Gaura odorata and G.
longiflora plants were especially attractive to the corn earworms and to other noctuids (Raultson et al., in review, Raven and Gregory 1972).

Several records exist for black cutworm and armyworm moth feeding. Armyworm has been found feeding on mashed and decaying apples and the nectar of catnip (Knight 1916). Many winter annual weeds and perennial trees bloom very early and may attract black cutworm for feeding and oviposition (Sherrod 1976). One of the most comprehensive records of black cutworm feeding was done in Missouri (Wynne and Keaster 1987) with observations from late April to October between the hours of 2230 and 0400 (CST). Attractive plants were: wild plum, Prunus americana (Marsh); crabapple, Malus sp.; common lilac, Syringa vulgaris (L.); autumn olive Elaeagnus umbellata (Thumb.); wild cherry, Prunus serotina (Ehrh.), amur maple, Acer ginnala; Russian olive, Elaeagnus angustifolium (L.); black locust Robinia pseudoacacia (L.); linden, Tilia spp.; privet Ligustrum ovalifolium (Hassk.); northern catalpa, Catalpa speciosa (Warde); goldenraintree, Koelreutaria paniculata; red clover, Trifolium pratense (L.); and common milkweed, Asclepias syriaca (L.). The flowers of linden were especially attractive. Further, all of the plants attractive to black cutworm were also attractive to the armyworm.

The European corn borer has not been recorded feeding on nectar. Moths were found to feed solely upon water, primarily in the form of dew (Drake 1926, Spencer and Crawford 1923). Drinking water is essential for good egg production and for satisfactory hatchability of the eggs (Kira et al. 1969). Honey has been added to the drinking water to increase production of eggs (Miller 1988). Four differences in favor of honey-
water feeding were found: a greater proportion of unlaied eggs were mature; fewer expired females contained immature oocytes; late eggs were heavier; and more females maintained or increased egg weight during the oviposition period. Female lifespan was shorter in the honey-water feeders. Although no reports could be found of European corn borer feeding, the borer has a well developed proboscis capable of nectar feeding (Miller 1988), and other pyralids are known to feed (Campbell and Pike 1985). Although not completely indicative of nectar feeding, two European corn borers were collected at a trap baited with the bladder flower, Araujia sericofera (Brot.) (Cantelo and Jacobson 1979). The bladder flower contains phenylacetaldehyde and attracts many nocturnal insects, including corn earworm and armyworm. Further, many other pyralids were also taken in traps baited with the bladder flower.

Several references have already cited insects feeding on milkweeds. Other studies have concentrated exclusively on insect pollination of milkweed. One of the earliest reported several Autographa precationis (On.) hanging dead by their proboscis or maxillae, caught by the pollen "trap" of an asclepiad (Packard 1880). Many researchers observe only diurnal feeders. For example, Macior (1965) and Lynch (1977) examined pollination of milkweeds by diurnal bees and wasps in detail. The European skipper, Thymelicus lineola, adult feeds frequently and becomes trapped in the milkweed by their legs or proboscis (McNeil 1977).

Milkweed nectar, however, is produced mainly between 1800 and 2200 hr for Asclepias verticillata (L.) (Willson et al. 1979). Similarly, maximum sugar content occurs at 2200 hr in Asclepias syriaca in Illinois
(Willson and Bertin 1979). Thus, many nectar feeders might be nocturnal, when maximum nectar flow occurs. When studying foragers, honey bees, *Apis mellifera* (L.), were the most common pollinators overall, but they forage during the day (Willson and Bertin 1979). With native pollinators, the Noctuidae comprised 39-52% of the pollinators. The variegated cutworm, *Peridroma saucia* (Hübner) and the black cutworm were often the most important native pollinators. The armyworm and *Leucania multilinea* were common during part of the study. Moths were also commonly found in *Asclepias verticillata* (Willson et al. 1979). Two noctuids, *Tarachidia candefacta* and *Alypia octomaculata*, were common during parts of the study by Willson et al. (1979). The black cutworm and *Autographa precationis* were also captured occasionally. All of these moths were reported as nectar thieves, however, with few pollinia transferred. This raises the possibility that natural selection might favor earlier nectar production to attract more honey bees (Bertin and Willson 1980). The nocturnal visitors removed fewer pollinia and inserted few pollinia when compared to diurnal feeders. However, seed set was equal for *A. verticillata* and greater for *A. syriaca*. The nocturnal feeders were, therefore, concluded to be higher quality pollinators than diurnal feeders (Bertin and Willson 1980).

Pollen carried on the moths can also be used as an indicator of flower visiting. Most research on pollen loads has centered on butterflies. Massive amounts of pollen were found attached to a *Papilio* butterfly (Poulton 1929). The pollen was unknown, but because of the location on the butterfly, it was concluded that the plant must be a lily
of some type. Similarly, *Papilio demoeus* often frequents the climbing glory lily, *Gloriosa superba*, and becomes contaminated with pollen in the same manner (Higston 1929).

More recently, workers have examined pollen loads carried by common North American butterflies. The wood white butterfly, *Leptidea sinapis*, was examined from several nectar plants (Wiklund et al. 1979). Although captured immediately after visiting flowers, a mean value of only three pollen grains was found on the butterflies. From this, the theory was advanced that butterflies, as a group, may have evolved to occupy a parasitic mode of existence as adults. This hypothesis was contradicted when four other common butterfly species were examined (Courtney et al. 1982). Pollen was commonly found carried on the facial cavity, where it was transferred on the coiling of the proboscis. Although not primary pollinators, the butterflies can act to some extent in pollen transfer. Regardless, the butterflies visited the plants and could be identified as having done so. Similar studies found flower visitation could be determined by pollen on the butterfly (Grace and Nelson 1981, Lazri and Barrows 1984).

In a study of hawk moth pollination, palynological analysis was used on the pollen loads (Kislev et al. 1972). Pollen yield per insect ranged from 2 to over 5000, averaging about 1300 grains. Two to 10 different types of pollen were carried on a single proboscis. Thirteen different plants were identified from the pollens and the flowers fell into two groups, those that are pollinated exclusively by the proboscis and those that are pollinated by other body parts as well. Corn earworms collected
in Arkansas were found to have pollen on 68.3% of the moths (Hendrix et al. 1987). Most of the pollen was on the proboscis (87%) or on the eye (11.8%). Pollens identified included legumes, composites, willow and evening primrose.

**Feeding studies in the laboratory**

Feeding studies in the laboratory allow greater control of the test insects. Studies can be conducted to elucidate feeding times and behaviors. Feeding after emergence is especially critical since it plays such an important part in migration and oviposition.

Female cabbage loopers were observed to feed an average of 2.2 times on the night following their emergence (Shorey et al. 1962). On the second night, they fed an average of 3.0 times. Males also fed frequently but were not itemized by the researchers. Laboratory reared corn earworm imagoes would visit feeders at least once on the emergence night, feeding from 1 to 3 min (Callahan 1958).

**Noctuid Migration**

**Migratory and life history strategies**

Because migration is particularly hard to understand and quantify, it has often been an overlooked component in insect dynamics. Migration has evolved such that insects migrate to find suitable sites for reproduction and food resources. Most pests of established annual agricultural crops
are migratory in nature (Taylor 1974). These pests utilize cyclical cropping systems and possess the ability to find new hosts (Taylor 1974). These insects have been viewed as being in an "oogenesis-flight syndrome" (Johnson 1969). Therefore, migration takes place before egg development and reproduction. Migration, consequently, occurs primarily in young adults and its chief function is to allow escape from unfavorable habitats and allow colonization of a broad range of environments.

Insect migrants are colonizers and not refugees (Dingle 1972). A successful migrant must be able to reproduce and leave viable offspring within the new habitat; the individual should have a high reproductive value when migrating. For insects exploiting a wide range of hosts, the primary risk of emigration, failure to find a suitable host, will be minimal. Selection, therefore, favors migration and the traits associated with rapid exploitation of a habitat's resources (Gatehouse 1987). Less obviously, migration often occurs while the insect is in adult reproductive diapause (Dingle 1982).

The theories of migration as a relief valve for overpopulation, a "pied piper" movement (Rabb and Stinner 1978), or even as simple diffusion until freeze-back in the fall (Walker 1980), have fallen out of favor as further evidence of migration has been provided. The "oogenesis-flight" (Johnson 1969) and the theories of Novák and Spitzer (1972) and Kennedy and Way (1979), concerning migration as ecological alternatives to diapause and unstable environments, seem to fit the case histories best. Noctuids offer a foundation and framework of case histories for these theories of migration.
Case histories and techniques

Until recently the bulk of evidence to support migratory claims was observational data. As technology has advanced, entomologists have discovered new methods to track migrating noctuids. These methods include trapping, mark-release-recapture, backtracking air parcel trajectories and mapping synoptic weather patterns, gene studies, insecticide resistance, and pollen analysis. A summary will be made of noctuid migration in general, followed by a more detailed examination of migration by the corn earworm, armyworm and black cutworm.

The simplest evidence for migration is observational. Some of the earliest records of observational data date from 1100 A. D. (Williams et al. 1942). These sightings record butterfly movements that would suddenly appear in large numbers, causing great consternation. These butterfly movements indirectly demonstrate one problem with monitoring noctuid migration; the migration of day-flying insects prove more noticeable than those of night-flying migrants.

The observational method for noctuids was, and is, especially popular with "gentlemen" scientists. The British, especially, have developed a large network of scientists and interested amateurs who collect and make observations every year. These surveys have provided invaluable baseline data (i.e., Bretherton and Chalmers-Hunt 1979, 1980, 1981, 1982, 1983, 1984). These data show distributional records and relative abundance during a single year. In addition, they can make comparisons between years and offer insight as to the possible circumstances which might allow transport.
After severe drought in the great plains (Texas, Oklahoma and Kansas) from 1931 to 1936, insects showed a marked tendency to extend their range to the north and east, becoming common in areas where they had once been rare (Bird 1937). A specific example was the corn earworm which appeared in unusually large numbers in Manitoba and caused considerable damage. During another season, a large aggregation of *H. zea* was observed at Boulder, Colorado (Cockerell 1914). These insects were thought to have travelled 1800 km. In addition, the northward movement of *H. armigera* in Europe to northern Germany from the south has been observed (Speyer and Speyer 1862).

The armyworm, a cosmopolitan noctuid, is reported from all of the major land masses of the world. It appears to be North American in origin, however, and reaches its destructive potential in this area (Breeland 1958). Because of the erratic nature and severity of outbreaks, there have been many published reports when it does occur in North America. The moths were thought to fly from the south in great numbers with the prevailing wind (Walton 1947). These outbreaks could be so severe to grasses and cereal crops that the armyworm constituted one of the most important insects attacking these crops (Guppy 1961).

One of the first recorded outbreaks (reported by Breeland 1958) occurred in 1817 in New York state. In 1896, a major outbreak occurred in the northeast and was the most destructive of any previously recorded (Slingerland 1896). Subsequently, in 1914 a major outbreak occurred throughout the United States and much of Canada, precipitating numerous articles in 1915 and 1916. Many moths were taken from 22-25 June 1914 in
New York (Knight 1916). Nothing unusual was noticed until July 14 when armyworm larvae suddenly began migrating across roads and destroying fields. Damages of $300,000 (Canadian) were reported from this outbreak in eastern Canada alone (Gibson 1915). Control of the pest was limited to digging trenches 25 cm deep in advance of the caterpillars' march. Massachusetts (Fernald 1914), Connecticut (Britton 1915), Indiana (Davis and Satterthwait 1916) and Ontario (Baker 1915) also published major accounts of this outbreak. Since then, several smaller infestations have occurred in the United States. In England, _P. unipuncta_ has been reported several times and is considered a rare immigrant (Bretherton and Chalmers-Hunt 1981, 1983).

In a similar manner, the black cutworm suddenly appears. The black cutworm is truly a cosmopolitan species and observational records exist from various parts of the world. Within the United States, an outbreak was reported in Oregon during 1919, where the moths were attracted to overflow lands (Rockwood 1925). Mass appearances were described in Soviet Georgia, Belgorod and Vorobeth Provinces and the Soviet Far East (Druzhelyubova 1976). _Agrotis ipsilon_ appeared suddenly in large numbers and caused the first economic losses attributed to this moth in Hungary (Mészáros and Nagy 1968). _Agrotis ipsilon_ was also recorded in Belgium (van Daele and Pelerents 1965), Sweden (Nordstrom 1943), and on mainland Iceland (Odiyo 1975). Further, they were found on the widely dispersed islands of Hawaii and the Galapagos (Williams 1911). In England, hundreds of _A. ipsilon_ moths arrived near Plymouth during October (Williams et al. 1942). More recently, the black cutworm has made
several notable appearances into the British Isles, migrating into the country from March until November (Bretherton and Chalmers-Hunt 1981, 1982, 1983; Classey 1983).

Entomologists in India commonly report observations of immigration into tal lands (overflow lands). Black cutworms migrate during summer months to adjoining low mountain ranges and return to the Indian plains in autumn (Singh 1949, Venkatraman 1954). Further, they breed freely in the hills during the summer (Fletcher 1925). Large numbers of frozen *A. ipsilon* have also been observed in India along the Rohtang Pass (Himalayas) at an altitude of about 4100 m. The moths were observed moving from the Kulu Valley into the hills and more northern valleys (Kapur 1955). Similarly, large numbers of black cutworm were discovered at 2300 m in Austria when temperatures averaged between 7 and 10°C (Mazzucco 1967). In Egypt, *A. ipsilon* were found to make mass flights in the spring along the Nile Valley and the coast of the Red Sea (Williams 1924, 1926). Also, large flights and many dead moths were found at the Red Sea (Bishara 1932). *Agrotis ipsilon* has often been cited as a migrant in Israel, where it passes though on a seasonal migration from the shores of Africa to the mountains in Lebanon (Rivnay 1964, Rivnay and Yathom 1966).

During the early part of this century, when travel by ship was popular, observations were made of moths captured many kilometers from the nearest land. Four moth species were taken 300 km SSE from the lower China coast (Poulton 1909). The wind was from the coast and, at 1000 hr, many small moths were observed to settle over the deck, all in perfect
condition. They were also observed to rest on the surface of the sea, even on broken water around the bows of the boat. The collectors noted, "what surprised us most was the beautiful condition so many of them ... were in, showing that their long journey had no ill effects upon them."

A migratory pyralid, *Nomophila noctuella* (Schiff), was observed resting on a calm sea (Poulton 1928). The ship was 670 km from port. A female hawk moth was collected while flying around the lights of a steamer in the south Atlantic, over 480 km from the Brazilian coast (Simes 1932). The oriental armyworm, *Leucania separata* (Walker), was reportedly taken more than 100 km from the nearest land on the Bohai Sea, China (Hsia et al. 1963).

*Agrotis ipsilon* has also been recorded several times in flight over an ocean. It was recorded at the lights of a ship in February 1957 when the ship was 500 km from the coast of New Zealand (Common 1958). It was also commonly observed at sea during February and March near New Zealand and under driftwood on the beach (Fox 1978). During 1968, *A. ipsilon* were collected from two weather ships about 500 km south of the Japanese mainland. These visits were common under the presence of a depression or front (Syoziro and Yasuaki 1970).

Using an unusual trapping method, migration has been examined by placing traps on unmanned oil rigs, many kilometers from the nearest land. Insects were attracted to lights at off-shore platforms 160 km from Galveston, Texas (Baust et al. 1981). Swarms of insects were detected moving in a southerly direction. Most of the moths arrived in single species swarms throughout the night, alighted for short periods
and departed, still in separate swarms. The noctuids captured were:
tobacco budworm, *Heliotris virescens* (Fabr.); granulated cutworm, *Agrotis subterranea* (Fabr.); velvetbean caterpillar, *Anticarsia gemmatalis* (Hübner); fall armyworm, *Spodoptera frugiperda* (J. E. Smith); *Semiothisa punctilineata* (Packard); and *Pseudoplusia rigationis* (Gn.). Baust et al. (1981) hypothesized these oil platforms offered "rest stops" and sources of fresh water from condensation.

One of the most notable reports on oil rigs was provided by Sparks et al. (1975). Four battery operated light traps were placed on rigs to sample corn earworm. These rigs were located ca. 32, 74, 106 and 160 km from shore. As expected, the traps located closer to shore captured the largest numbers. Even at 160 km, however, three corn earworms were collected. An important and often overlooked fact concerning the study was that captures were made in September and could be indicative of a return migration to the overwintering sites in the south. Also, armyworms were collected 106 km and *A. ipsilon* 160 km from shore (Sparks 1979). Moths were collected from an oil rig 40 km west of New Zealand (Fox 1978). Most of the specimens collected were *A. ipsilon* and occurred from the middle of January through the middle of April.

Overwintering studies also provide circumstantial evidence for migration. Within the United States, overwintering experiments have been carried out for a variety of noctuid pests. The overwintering potential of fall armyworm in Kansas was observed by caging larvae and making field inspections for live overwintering pupae (Smith 1921). None were found to overwinter. The author concluded that the moths migrate northward
from the south in the spring. The fall armyworm is limited to southern Florida and southern Texas during cold winters, but can spread as far north as Ontario, New York, Minnesota and Montana (Snow and Copeland 1969, in Pair and Sparks 1982). To test this hypothesis, winter survival of pupae was tracked in several locations in Florida. It was determined that, although no diapause or cold resistant stage could be found, the fall armyworm could survive most winters throughout Florida (Wood et al. 1979).

The velvetbean caterpillar was tested under similar experimental conditions in southern Mississippi (Buschman et al. 1981). Pupae held at 9°C in the laboratory or in overwintering field cages died before spring. Further, emergence traps placed over areas known to be heavily infested with larvae during the previous fall failed to produce adults. Again, these moths had been recorded as far north as Canada, and their arrival is associated with southerly winds. The failure of velvetbean caterpillar pupae to overwinter in Mississippi and the arrival of adults far to the north in spring and summer generated the hypothesis that moths may be carried from south Florida or the Yucatan Peninsula into Mississippi (Buschman et al. 1981).

In China, attempts were made for 10 yr to find the overwintering sites of oriental armyworm in Northeast China. Many thousands of acres were examined and not a single armyworm was found. Further, field breeding experiments failed to overwinter this insect. The cold tolerance of this species, therefore, was determined to be very low (Lin et al. 1963).
Although the corn earworm can pupate and withstand some freezing temperatures, its northern distribution is limited. The corn earworm is unlikely to survive winters north of latitude 35°N in the central United States (Blanchard 1942, Metcalf and Flint 1951, Snow and Copeland 1971). Yet, corn as far north as Canada (52°N) is regularly infested with corn earworm in mid to late summer (Hardwick 1965). Therefore, the earworm extends its range 600 to 1200 km a year (Raulston et al. 1982). It is thought that the emigrations from the south are the sources of infestations found in the north (Blanchard 1942). Work in Virginia found 4 June was the earliest observed emergence date in the area (Dicke 1939). Eggs, however, were found in mid-May indicating immigration. Corn earworm also failed to overwinter at Ames, Iowa in screen cages (Hutchins 1935). Further, all pupae dug from cornfields during March were dead.

Overwintering studies with *P. unipuncta* have produced circumstantial evidence of its migration. Greater than 50% survival of pupae was found in Tennessee (Breeland 1958). Using identical cages, researchers were unable to carry any pupae through the winter in Quebec (Fields and McNeil 1984). Evidence for diapause or cold hardiness could not be found.

Likewise, overwintering studies with *A. ipsilon* have yielded important data. Attempts to carry late-emerging adults and pupae through the winter in Kansas failed (Walkden 1950). Larvae, pupae and adults were placed in dry vermiculite in an unused shed in Wisconsin. None survived the winter there (Apple 1967). Attempts to overwinter all stages of black cutworm in plots containing corn, timothy, alfalfa, foxtail and smartweed failed in Iowa (Carey and Beegle 1975). Likewise,
overwintering trials with *A. ipsilon* in field cages in central Missouri failed (Story and Keaster 1982). Similarly, *A. ipsilon* failed to enter diapause under any experimental condition tested by researchers in Japan (Matsuura and Miyashita 1978).

Circumstantial evidence for migration may also be provided if large increases in trap captures are noticed that do not fit in with known population dynamics. Reports of oriental armyworm appearances in early spring at successive and intermittent peaks coincided with the simultaneous appearance of southerly winds (Lin et al. 1963). Further, the dates of peak appearance differed by only 1-3 d throughout all of northeast China. It was concluded that the moths were from the same source regions and were carried by the same winds.

Several researchers examining the overwintering potential of the corn earworm have discovered pheromone traps capture males before any local moths can be found emerging from observational chambers. The first egg peak of tobacco budworm occurred about 25 d before peak emergence from diapause (Raulston 1979). Further, pheromone trap catch preceded the emergence peak by about 10 d. Blacklight captures of corn earworm preceded the emergence of local moths in Stoneville, Mississippi by a month or more (Stadelbacher and Pfrimmer 1972).

A major migration of corn earworm adults was tracked in 1981 by pheromone traps (Hartstack et al. 1982). Peak pheromone trap catches were 19 d before peak emergence in College Station, Texas and 33 d ahead of local emergence in Portland, Arkansas. The peak trap catches generally became smaller the farther north the traps were placed,
suggesting a possible dilution of moths as they spread northward. In a similar case, examination of corn earworm immigration into Arkansas later in the season found trap capture on 1 July 1982 occurred at a time when no population could have been produced locally. It was this immigrant population that necessitated the first widespread H. zea insecticide treatment in southern Arkansas, thereby demonstrating the economical importance of immigration (Mueller et al. 1984).

A lack of synchrony was noted between first capture dates for P. unipuncta and the emergence of closely related indigenous species. These dates may differ by more than 3 wk (McNeil 1987). Analysis of light trap catches from 1921-1931 in Kansas consistently found the first species to be taken in the traps each spring were A. ipsilon and P. unipuncta (Walkden 1937). They were also the last to be taken each fall.

A method closely related to trap monitoring is the biogeographical technique. Here, the distribution of noctuid moth species are monitored and mapped, thus predicting seasonal changes. The successful utilization of this method led to the tracking of African armyworm, Spodoptera exempta (Wlk.). In eastern Africa, these biogeographical studies were first undertaken during 1961-1969. Analyses of the data suggested a seasonal outbreak northwards from Tanzania to Kenya, Ethiopia, Yemen, and southwards through Zimbabwe to South Africa (Brown et al. 1969). This outbreak was associated with the movement of the Inter-Tropical Convergence Zone (ITCZ) and the rainy season within these countries. This hypothesis of continuity of movement with the ITCZ from country to country was an important step forward in the development of a regional
strategy (Rainey and Betts 1979). The data suggested that spread could be limited by controlling any previous outbreaks (Rose et al. 1987). Based on biogeographical techniques, an accurate forecast for the cross-border migrations of moths between three African countries led to the effective control of larvae to save cereal crops, sugarcane and pasture in East Africa (Odiyo 1987). A detailed biogeographical examination of A. ipsilon, tracing its movement throughout the year on a world-wide scale, gives credence to the hypothesis of black cutworm movement from warm areas into more temperate climates, during the summer (Odiyo 1975).

In another variation of trapping studies, scientists have placed traps at various heights above ground. If moths were collected many meters above the insect boundary layer, the hypothesis was that the insects were in a migratory stage. Use was made of blacklight lamps set at various heights above the ground on a telephone pole and a fire-lookout tower (Stewart and Lam 1968). Of note, the catch of armyworm generally increased with the height of the trap. The cabbage looper, however, was collected only above 17 m. The black cutworm, the yellowstriped armyworm, Spodoptera ornithogalli (Guenée), and the corn earworm showed no consistent trends in catch with height. Although the highest trap was only 30 m above ground level, it is evident the above noctuids were moving a great distance above the plant canopy (a tobacco field). In comparison, three species; the saltmarsh caterpillar, Estigemene acrea (Drury), and two species of May beetles were taken only below 17 m. Traps placed at 15 levels (between 8 and 319 m) on a
television tower commonly collected corn earworm moths above 84 m and as high as 305 m (Callahan et al. 1972).

Several air borne sampling programs have been undertaken with noctuids. The most famous were the collections made by Glick (1939, 1957) and Glick and Noble (1961). During a night flight, in a field over Louisiana, 10 different species of noctuids were collected, including a corn earworm at 152 m (Glick 1939). Also, one cotton leafworm moth *Alabama argillacea* (Hübner) was taken at 920 m during the day. Flights over the Rio Grande area of southern Texas collected a single noctuid, a cabbage looper (Glick and Noble 1961). In a variation of this technique, kites and tow lines have been used experimentally to sample from the air. This technique has proved of limited usefulness, especially with night-collected samples where it was difficult to determine the status of the kite (Farrow and Dowse 1984).

The above studies of aerial trapping offer several benefits, such as allowing sampling at heights greatly above those taken from pole samples. Using these procedures, one can take samples from many different areas and above a variety of habitats. The altitude of collection can be measured and samples can be labelled with time periods to show periodicity of flight. Further, samples can be made during the day or night and insects that might not normally be attracted to the light traps could be collected. However, air sampling is not without its drawbacks. Air sampling is expensive, and a large volume of air must be sampled to collect even a few insects. Trap design is also a problem because many insects are easily destroyed. Sampling frontal movements, thought to be
an ideal location for migrant noctuids, is prohibited because of the danger to the plane and pilot.

Although Glick and coworkers sampled from the air, many of the specimens were damaged. The scientists could not determine if the insects survived travel at such high altitudes (Glick 1939). However, when testing the effects of high-altitude exposure upon survival of tobacco budworms, exposure to climatic conditions at altitudes from 1.2 to 2.4 km above sea level did not significantly reduce the capacity of unmated moths to mate and reproduce (Hendricks 1983). Furthermore, nearly one-half of the previously mated females laid fertile eggs and could contribute to the population dynamics after a long-distance migration. Most important, the moths were able to maintain a directional bearing by perceiving some unknown standard.

Although able to withstand the hardship of high altitude flight, little was known until recently about the movement of insects within the air. One of the first papers published on insect dissemination by air currents used balloons to study air movement (Felt 1925). Insects might be carried to elevations exceeding 300 m and may drift 1287 km within a 24 hr period. Insect flight is rarely observed at sunset but numerous species commence migrations soon afterward in a dusk takeoff flight (Drake and Farrow 1988). These flights continue for several hours and occasionally last until dawn. Many of the larger migratory species can attain altitudes of 500-1000 m in less than 1 hr under these conditions. Night-time conditions may be especially favorable for any type of migratory flight because of a lack of predation and/or lack of thermal
stress. Further, migratory insects are likely to become concentrated in zones of convergence that may persist for some time (Drake and Farrow 1988).

Trajectories can be made of possible flight patterns from synoptic weather maps because many studies are initiated after the influx. For example, a mass immigration was observed and a backtrack made to see where the moths might have originated. To backtrack, surface (100-300 m) and 850 mbar (= 1500 m) trajectories generally provide adequate information on windspeed and direction so that one can arrive at a fair approximation of the flight track for insects travelling between the earth's surface and 1500 m. Radiosonde ascents and reported weather along the route were used to fill in details on the vertical profiles of wind and temperature. Further, the presence of low-level jet streams should be taken into account. The analysis, however, can only suggest a corridor containing the probable flight track and source region (Rose et al. 1975). Collectively, the most important aspect for migration within the United States is the atmospheric pattern of high pressure along the east coast of the United States and a low pressure over the Great Plains. Further, a frontal system is frequently present in the landing area which may act as a barrier to additional migration (Scott and Achtemeier 1987 and others listed therein).

Several examples exist of backtracking over the continents. A large immigration of fall armyworm which suddenly appeared in Sault Ste. Marie, Canada was backtracked (Rose et al. 1975). The weather reports showed that a minor trough of low pressure passed over Sault Ste. Marie during
the time of the sudden appearance. The trough was associated with a line of convergent winds at the surface and a low-level jet at 1000-1500 m. The flight was backtracked to the Illinois-Wisconsin border. No heavy infestations, however, were reported, nor were there significant light-trap catches. The next possible source region was in Mississippi, which had been reporting heavy infestations for some weeks. The moths were able to cover this distance in 2-3 d. In another study, analysis of _Pseudaletia separata_ captures suggested two waves of moth immigrations carried by cyclonic winds in northern Japan (Kazuo et al. 1985).

In Britain, the possibility of long-distance windborne movement by _Heliothis armigera_, from southern Europe into Britain, was examined (Pedgley 1985). Of 28 possible immigrations, the author found that 22 were associated with spells of southerly winds created from the influence of large anticyclones centered over central or eastern Europe. The author also noted a migration into Finland following 4 d of south and southwest winds. When backtracked, the trajectories showed a distance of 2000 km. In a similar study, examination of _H. armigera_ movement in the Middle East found that moths were brought into Cyprus, Turkey, Lebanon, Israel and Sinai on spells of southeast winds that lasted several days (Pedgley 1986). The source region might have been Saudi Arabia, 1000 to 2000 km away.

Of a much more difficult nature was the determination of _Heliothis_ migration into an area where it already occurs. For example, migration of _Heliothis armigera_ into India was studied (Pedgley et al. 1987). Because India is basically surrounded by possible inocula, immigration
was difficult to determine. Circumstantial evidence of migration was provided by evidence that trap catches would increase with winds originating from areas that had large populations of *H. armigera*. Likewise, analysis of circumstantial evidence could not determine if migration was occurring regularly into Arkansas; movement was thought to probably occur into, as well as out of the state, but no net change would exist in most cases (Phillips 1979).

Several examples of migration over large bodies of water also exists. One example is a backtrack of the armyworm, *Spodoptera exigua* (Hb.), which covered 3000 km, mostly over the sea. The moth originates in Portugal, Spain and North Africa. Yet, they regularly fly northwards to northern Europe (Bowden and Johnson 1976). In another example, a trans-Atlantic crossing (over 3200 km) of *Phytometra biloba* (Steph.) was backtracked (Johnson 1969). This noctuid is native to North America and is not found breeding in Europe or Africa. Backtracking the winds, a satisfactory fit was made to an origin in Virginia with a flight time of 3.5 d.

Backtracking the movement of black cutworm and analysis of complementary synoptic weather charts has been examined by several researchers. One of the first studies looked at migrations into Finland for 52 species during 1946-1966 (Mikkola 1967). Several migrations of *A. ipsilon* were recorded during this period. Movement into Finland often came from the southwest, from Russia, on anticyclonic movement. A three-day flight of *A. ipsilon* from the Morocco area into England during 1962 was also backtracked (Hurst 1969). Invasions by *A. ipsilon* in the Near
East were discovered to be associated with some of the same depressions that brought locusts across distances of 3000 km (Rainey 1974).

In the United States, the spring weather pattern associated with black cutworm introduction into Iowa was examined (Domino et al. 1983, Showers et al. 1986). A meteorological rating system based on environmental factors such as strong southerly winds and high pressure systems was developed and utilized by the researchers. This system has greatly aided prediction forecasts for this pest in the central United States. In an effort to verify the rating system, results of a mark-release-recapture study, made in conjunction with air-parcel trajectories analysis, were reported (Showers et al. 1989a). The trajectories from the surface level produced the best fit for transporting marked males from Louisiana and Texas to Iowa. The air flow needed for transport was provided by a series of low-pressure systems to the north and west of the migration path. This synoptic condition would serve as a pump capable of inducing air flow to move northeastwardly through a narrow corridor. As an important point, it was noted that movement at levels other than the surface were possible but would carry the insects out of the recapture area (Showers et al. 1989a).

Although a very important method of tracing the long-distance movement of noctuids, backtracking is not without its hazards. A review of back-track analysis found that errors in a 24-h back-trajectory might vary endpoint locations from 0 to 250 km or more depending on persistence of wind (Scott and Achtemeier 1987). Events, such as short-lived nocturnal jets, may pass through their cycle between regular upper air
observation times. In these cases, large errors between the calculated back-trajectories and the actual migratory path occur. Combination of back-track trajectories and other methods, such as mark-release-recapture (see Showers et al. 1989a, Showers et al. 1989b), help overcome these obstacles.

Entomological radar was used to observe insect activity in northwestern Tasmania during the spring of 1973 (Drake et al. 1981). Insects were found to regularly take off at dusk and local movements could be observed using this technique. Large-scale movements across the Bass Strait were also observed and found to be associated with anticyclonic airflows which occurred ahead of a cold front. Light-trap captures made in conjunction with the radar study indicated the insects were noctuid moths, with *Persectania ewingii* (Westw.), *Heliothis punctiger* (Wllgr.) and *Agrotis munda* (Westw.) dominant. Using radar, this time in New South Wales migrating populations were frequently found to exhibit a degree of mutual alignment (Drake and Farrow 1985). Migrants became concentrated into layers at high altitudes on two different nights; these layers were oriented with the wind and were moving towards the south pole.

A similar phenomena was reported over an Arizona cotton field (Wolf 1979). During 4 April 1979, insects were detected in three distinct layers. The first was very thin and 310 m above the ground. The insects in this layer were oriented randomly. The middle layer was between 660 and 940 m and most of the insects were oriented north-northeast, with the wind. The upper layer was 1250-1380 m above the ground. Orientation was
again toward the northeast. Insect density usually increased rapidly with height within an inversion layer, and then decreased more gradually with height at higher levels (Drake 1984).

In a similar study, an early evening flight initiation with a rapid ascent to 600 m was described, followed by formation of an insect layer within 2 hr after sunset (Wolf et al. 1986). Some insects began a descent 4.5 hr after sunset. Significant numbers were reported to ascend to 1000 m in less than 1 hr. When insect layers were detected, the layering began within 3 to 4 hr after sunset. On at least two nights, this pattern persisted until dawn. The time of layer formation and the position of layers near the centerline of low-level jets suggested that the physical properties of these jets contributed to layer formation, or, conversely, that the insects somehow detected the layer and flew in these jets.

Radar has been used to observe flight behavior of the armyworm at an emergence site (Riley et al. 1983). Almost all of the emergent moths climbed to altitudes of several hundred meters and migrated from the emergence sites. But, on other occasions, the moths roosted in trees until dawn, then engaged in short dispersal flights until dusk the following night, when they began a mass migratory flight.

Complications arise from radar research, however, because of the limited mobility of radar. Radar observations also lack detail for species identification. Verification of species has been done on the ground where specimens can be observed individually.
Mark-release-recapture studies have greatly aided migration research. Because the insects are released at a known point and recaptured at a known point, distance can be calculated with certainty, offering conclusive evidence for migration. Flight patterns of natural migrating populations can be discovered and extrapolated from backtrack trajectories. There are various methods of marking the insects.

Naturally occurring African armyworm moths were marked with dyed molasses (Rose et al. 1985). In all, 166,000 moths were estimated to have been marked upon emergence. Six marked moths were captured in pheromone traps, including one at 90 km and another at 147 km. Movement was downwind and some of the moths were ready to mate on the same night they completed their long-distance flight. Using radar and synoptic weather charts, they determined the moths began flight at dusk and flew to heights up to several hundred meters where winds of 30 km/h or more occurred.

Insects may also be marked with various compounds. Corn earworm and fall armyworm were marked with rubidium for dispersal studies (Graham et al. 1978). Male cabbage looper moths were recovered 3000 m from the release point after being marked in similar manner (Henneberry et al. 1967). Another method of examining insect populations is use of elemental compounds (chemoprints) taken up in host plants from the soil. Although of some value, this method is often confounded by elements already in the food plants (Sherlock et al. 1985). Certain fatty acids found in adults may be indicative of migration if immigrant larvae were reared on different host plants from non-migratory counterparts (Bridges
and Phillips 1972). While it was true that certain fatty acids could be associated with specific host plants, the technique proved too expensive to be practical for migratory studies.

*Spodoptera littoralis* (Boisd.) adults were marked with Calco Oil Red dye, an oil soluble dye which marks the fat body (Kehat et al. 1976). In all, 28 males (7.2%) were recaptured at a distance of 350 m. Empirical evidence for migration of the oriental armyworm was provided by marked moths released in China (Li et al. 1964). From recaptures, they were able to trace the northward movement in the spring and a return flight in the fall. Laboratory-reared *H. virescens* adults were marked with dyes fed to the larvae (Hendricks et al. 1973). The moths were released in Mexico and dispersed 16.1 km north in 24 hr. In southern Texas, moths dispersed as much as 112.6 km in an estimated period of 4-5 d. In a similar study, tobacco budworms and corn earworms were reared on diet containing dye (Haile et al. 1975). These pupae were sterilized by radiation and released in St. Croix, U. S. Virgin Islands. Marked male moths of both species were captured on Vieques, 68 km away, and tobacco budworms were recaptured on St. Thomas, 61 km away. Further, four red tobacco budworm eggs were found on Vieques, thus proving that the females released on St. Croix were capable of reproduction after their journey. Approximately 250,000 internally marked, sterile male and sterile-male-producing female *H. virescens* were released in the Delta of Mississippi during 1982 and 1983 (Schneider et al. 1989). An extensive grid system of traps was established to monitor the movement of the moths. By estimating the relationship between trap catch and density, the authors
concluded that 70% of the released population moved out of the study area (18 km).

Black cutworm moths have been used in several mark-release-recapture studies. *Agrotis ipsilon* moths were marked and recaptured at distances of 1818 km from the release site in China (Jia and cooperators' 1985). The recapture of marked *A. ipsilon* from release sites in Louisiana and Texas has also been described (Showers et al. 1989a, Showers et al. 1989b). The moths moved distances of 1266 km from the release site in an estimated 2 to 4 nights.

Problems with mark-release-recapture studies arise because the insect is altered in some way to mark it. Most are laboratory reared and may not reflect natural populations. One of the most serious drawbacks is the large numbers of insects needed in order to recapture moths over any distance. The greater the migratory distance the larger the area needed for sampling.

In contrast to mark-release-recapture studies, some researchers have examined intrinsic differences within the populations themselves. Largely, this is very time consuming and expensive. It can help define the amount of interaction between moths captured in various locations of an insects' range. Morphological comparisons of male genitalia of *H. zea* were made of moths collected from Texas, Mexico, Arkansas, Louisiana, and Missouri (Phillips 1979). Several Arkansas moths appeared more similar to Mexican moths than to those from any other location when the morphometric comparisons were analyzed. However, nothing positive could be concluded.
Flight mills and tethered flight can produce information about flight duration, fat consumption and dispersal potential. Although innovative, the work is hindered because the insects are often subjected to artificial conditions and most specimens are laboratory reared. But, many variables such as crowding, daylength and energy utilization can be controlled and examined. The army cutworm, *Euxoa auxiliaris* (Grote), was studied on a flight mill (Koerwitz 1961). The mean duration of individual flight for laboratory moths was 5.4 hr, while the maximum duration of flight was 23.3 hr. Moths captured from light traps flew a mean time of 10.7 hr and generally adapted more rapidly to the artificial flight conditions. Speeds attained ranged from 1.0 to 4.8 km/hr.

Examination of female *Plusia gamma* L. flight in the laboratory found that during the first three days of adult life, the females were almost continually flight active (Macaulay 1972). Flight was not inhibited by high light intensity as it was in older moths. The celestial orientation of the large yellow underwing moth, *Noctua pronuba* (L.), was studied using a semi-automatic flight monitor that permitted recording of the orientation of flight (Sotthibandhu and Baker 1979). On moonlit nights, the moon's azimuth was used as an orientation cue. In absence of the moon, stellar orientation using stars was implicated. The moths became disorientated in a dark room or when their eyes were painted over.

Larval crowding and flight has been investigated by using flight mills with the black cutworm (Lewis and Keaster 1986). A microcomputer-interfaced flight mill system for large moths has also been developed (Resurreccion et al. 1988). Thirteen laboratory reared male black
cutworms, secured at the thorax with rigid or flexible tethers, were compared for distance traveled (9.55 km) and average velocity (2.04 kph) (Resurreccion et al. 1988). Tethered *A. ipsilon* and *A. segetum* were found to have inheritable flight ability (Blair 1978). Active fliers mated with active fliers produced active offspring. Similarly, inactive fliers produced inactive offspring.

Ovarian status and degree of body fat depletion of female moths can be used to determine migration. Investigations in Iowa of green cloverworm, *Plathypena scabra* (F.), reproductive condition found females captured during the early spring flight progressed from ovipositional to postovipositional (Buntin and Pedigo 1983). Unmated, preovipositional females were not captured. Further, late season females were preovipositional. These results might be indicative of a fall migratory phase (i.e., oogenesis-flight syndrome (Johnson 1969)). Adult celery looper, *Syngrapha falcifera* (Kirby) phenology progressed in a like manner (Peterson et al. 1988). The first trap catches in mid-April revealed only ovipositional and postovipositional females. This finding strongly suggests that overwintering does not occur in Iowa or some preovipositional females would be found.

In an analogous situation, most Canadian *P. unipuncta* females in mid-May through July had well-developed ovaries and had mated at least once (McNeil 1987). During the late season flight, however, the majority exhibited little or no ovarian development and were seldom mated. Similarly, a great many armyworm females in Iowa were found to be
sexually immature in the fall, while females examined in May contained fully developed eggs (Gillette 1890).

The ovaries of migrating black cutworm females collected at Rohtang Pass, in the Himalayas, were discovered to be undeveloped and the abdomen filled with fat (Kapur 1955). The ovaries were also undeveloped in moths collected from oil rigs 40 km off shore in New Zealand (Fox 1978). Agrotis ipsilon females that migrated into Central Europe from April and July were noticed to lay fertilized eggs immediately (Novák and Spitzer 1972). But adults that emerged in August and September had "unripe" ovaries, did not lay eggs and disappeared in October and November. Fall collected black cutworm moths from England would not mate or lay eggs (Bretherton 1969). Dissection of the females showed them to be sexually immature. Moths collected during the summer, however, readily laid eggs. Females collected in the fall from Bohemia (Spitzer 1972) were sexually immature as were moths collected in Egypt (Williams 1926).

A similar condition for black cutworms collected in Iowa was reported: fall females were sexually immature (Gillette 1890). Another Iowa study found all of the first-flight A. ipsilon females are mated, "a condition often associated with immigrating females" (Kaster and Showers 1982). A reproductive diapause was also found in fall populations. Likewise, females captured throughout the central United States in late September during 1978 and 1979 were young, unmated individuals (Levine et al. 1982). Further, males were not attracted to traps baited with females. In a corresponding study, similar results were found for Ohio (Clement et al. 1985). The issue of ovarian development in relation to
migration has been addressed; females would have two nights to migrate before becoming sexually attractive. Thereafter, the females would have one to three nights for copulation and one more night to continue the migration to the Corn Belt (Mulder et al. 1989). An alternate hypothesis is the moths might arrive unmated and not be initially attracted to the light traps (Showers et al. 1989b).

If large scale migration is occurring within a given population, susceptibility to insecticides should be similar throughout the range. If migration is not occurring, however, populations exposed to repeated insecticides should show different susceptibility than populations in infrequently sprayed crop areas (Taylor and Georghiou 1979). Pitre (1988) looked at fall armyworm from Florida, Honduras, Jamaica, and Mississippi. Of note, the Mississippi population was more similar to test populations from Jamaica and Honduras than the population from Florida. These results suggest that fall armyworm immigrating into Mississippi did not originate in Florida, but might have originated further south. This finding confirmed the hypothesis by Young (1979).

Pesticide resistance has been used as an indicator for corn earworm migration (Phillips et al. 1968). During 1967, seasonal collections were made throughout the state, including areas with both high and low pesticide usage. Results showed that, in Arkansas, H. zea populations response to insecticides was thoroughly mixed.

Genetic differentiation other than insecticide resistance have also been examined to determine likely migratory pathways. Velvetbean caterpillar specimens were collected from the southeastern United States,
Mexico, and Central America in an attempt to characterize each location, and 28 enzyme loci were examined electrophoretically (Pashley and Johnson 1986). Populations collected in Louisiana and Central America were identical to each other at all loci but different from populations in South Carolina and Florida. Populations from Florida were most distant and this analysis supports the divergence of the Florida populations. Large genetic differences among populations suggest low levels of gene flow, and therefore, a lack of migration. Equally important, the differentiation suggests that the southcentral United States population of velvetbean caterpillar may originate in Mexico rather than from overwintering populations in southern Florida. In a comparable study, complementary results were found (Hammond and Fescemyer 1987).

**Pollen analysis**

Only mark-release-recapture studies and pollen analysis currently offer direct evidence for migration. Pollen analysis is useful because many plants depend on insects for pollination and accordingly have evolved pollen that adheres readily to the exteriors of insects. Pollen can be identified at least to family and the geographic origin of the plants can be traced. Therefore, the origin of the moth can be determined. Unlike recaptured moths from mark-release-studies, moths dusted with pollen are naturally marked. Identification of the pollen however, is a major stumbling block to utilization of this technique. Pollen analysis has been used for studies of immigrants. Pollens were removed from dried museum specimens and examined (Mikkola 1971). Six A.
were studied and a single pollen grain of *Corylus* was found. In total, 13 species were searched for pollen. Inconclusive evidence was provided because the plants were not distinctive enough between the origin site and deposition site of the migrants.

Other palynological studies have shown the usefulness of pollen analysis in insect studies. A direct method of pollen grain identification was developed whereby the proboscis or head of the moth could simply be coated in gold and examined under the scanning electron microscope (Turnock et al. 1978). Other researchers have utilized this method for examining potential migrant moths (Courtney et al. 1982, Hendrix et al. 1987, Bryant 1989).

Pollen was used as an indicator of the long-distance movement of *H. zea* into Arkansas (Hendrix et al. 1987). Two Mimosoideae legumes, *Pithecellobium* and *Calliandra*, were discovered on spring migrants.

*Pithecellobium* is a shrub or tree with flowers in spikes or in heads. Three species of *Pithecellobium* occur in Texas, *P. flexicaule* (Bentham), *P. dulce* (Roxb.) and *P. pallens* (Bentham), and their distribution is centered around the Gulf Coast of Texas and south (Turner 1959, Isley 1972). All three species are in bloom during April and May when immigration occurs. Four other species occur in tropical Florida with other species widely distributed in the drier regions of the tropics (Long and Lakela 1971). The pollen is a polyad with 16 cells (Sorsa 1969).

*Calliandra* is a low perennial herb or shrub. Four species occur in Texas, *C. biflora* Tharp, *C. conferta* Benth., *C. eriophylla* var.
chamaedrys Isley, C. humilis Benth. (Turner 1959, Isley 1972). Again, the distribution is along the coast and Rio Grande and all species are in bloom during immigration periods. The pollen is a bilateral, flattened octad (Sorsa 1969).

Pollination biology of these legumes is not well defined. However, it is important that all of the polyads from Hendrix et al. (1987) were attached to the compound eye of H. zea and in the same general location on the eye, offering clues as to the pollination mechanism. In C. haemaocephala (Hassk.), a related Calliandra, the anthers are attached on the back in a median position at right angles to the axis of the filaments. Thus, the face of the anther is directed away from the center of the inflorescence. Each polyad is composed of two median pollen grains and six peripheral ones. One of the peripheral grains (foot grain) is modified slightly with a pronounced projection. The two polyads in an anther have the foot grains directed toward one another. Between the apices of the foot grains an extremely viscous substance is formed. When the polyad pairs are separated the sticky apices are rotated until they are directed away from the anther by at least 90 degrees. At anthesis the polyads are held with their apices directed outwards, and each apex is covered by a glistening drop of adhesive material to attach it firmly to the pollinator. The average inflorescence has some forty flowers and approximately 25 anthers per flower making nearly 8000 polyads available for pollination (Nevling and Elias 1971). Calliandra is moth pollinated and the Calliandra flowers were examined for the presence of moth scales (Cruden et al. 1976).
Pollination was compared against elevation and both flowers visited and pollinated decreased with elevation. Unfortunately, no study was made to determine the pollinators. In examining nectar production, the flowers of *C. anomala* produced large volumes of nectar (Cruden et al. 1976).

Like *Calliandra*, *Pithecellobium* is also pollinated by night-flying insects (Janzen 1982). Field observations found the nectaries very active in the evening and early morning (Elias 1972). Further, the activity of the nectaries coincides with pollen maturation. Activity ceases after pollination or fertilization. Flowers of *P. saman* begin to open daily at 1500 hr and most are open fully by 1700 hr. Nectar flow begins between 1600-1700 hr. Mean nectar production per inflorescence averaged 14.5 microliters (Jones 1983).

In total, 18 moths were collected with these exotic pollens adhering to the eyes or proboscis (Hendrix et al. 1987). These results prove migration of 1000 km or more.

In summary, it is critical to understand both field and laboratory behavior of adult noctuids. The purpose of the adult eclosion research presented in this dissertation was to examine the daily rhythm of emergence as well as the emergence cycle of the black cutworm and armyworm. Another purpose of the experiment was to discover if emergence differences exist between colonies held for approximately 6 and 18 generations in the laboratory. Cold storage has commonly been used to delay adult emergence for mark-release-recapture studies. Variations in emergence could have consequences for flight takeoff and moth survival. Therefore, a third purpose of the study was to determine whether pupae
held in low temperature (18° C) storage influenced moth emergence. Nectar taken by the moths can be used for long-distance flight or for production of eggs. The purpose of this part of the research was to find common plants that attracted nocturnal moths and to observe the feeding. Laboratory experiments would provide information concerning the timing of feeding. The purpose of the migration research was to use pollen analysis to study the migration of these pests. Moths would be collected from the spring and early summer immigration periods and examined for the exotic pollens discussed above. Information collected could help determine the important origin sites for immigrant moths into Iowa.
PART I. DAILY TIMING OF ADULT ECLOSION FOR BLACK CUTWORM,

AGROTIS IPSILON (HUFNAGEL), AND ARMYWORM,

PSEUDALETIA UNIPUNCTA (HAWORTH) (LEPIDOPTERA: NOCTUIDAE)
INTRODUCTION

Little is known about the daily emergence patterns for insects and what effect laboratory conditions might have on periodicity of emergence. Timing of emergence is critical for most insects and daily rhythms vary widely with species (Scott 1936, Dreisig 1986). Little is known of the effects laboratory conditions might have on these daily rhythms or on population cycles.

In the laboratory, the defoliators Halisidota argentata (Pack.) and Nepyia phantasmaria (Stkr.) emerged at the onset of darkness. If pupae were placed in constant dark, the emergence interval was primarily 1600-2200 hr (Edwards 1964). In studies with Ephestia kuhniella (Zell.) it was found that light variations, independent of any associated temperature variations, can cause changes in the emergence rhythm (Moriarty 1959). Emergence was not dependent on light conditions during the earlier stages of larval development (Giebultowicz and Cymborowski 1976). The later stages of development were synchronized with a biological clock regulated within the brain. Experimentation with the pink bollworm, Pectinophora gossypiella (Saunders), showed emergence in the laboratory and field to be between 0700 and 1000 hr. Smaller peaks occurred between 1400 and 1700 hr and 1800 and 2100 hr (Lingren 1983).

Studies of gypsy moth, Lymantria dispar (L.), emergence, under a photoperiod of LD 16:8 with lights on at 0600 EST found emergence occurred within 10 hr after the onset of light (Ma et al. 1982). Peak eclosion time for males was 3.14 hr after the lights came on, while
females peaked at 5.34 hr. Eclosion occurred within a specific period or "gate". If developing adults were not at the correct development stage, they remained in the pupal skin until the next period on the following day.

Eclosion of noctuids has been observed in several species. Emergence of laboratory reared cabbage loopers, *Trichoplusia ni* (Hübner), was found to be primarily during the daylight hours with a majority emerging in the morning (Shorey et al. 1962). In contrast, corn earworm, *Heliothis zea* (Boddie), emergence occurred primarily during the night and very early morning for laboratory-reared specimens (Quaintance and Brues 1905). Further, 94.6% of corn earworm emergence occurred between 1900 and 2300 hr in the laboratory, with 38.2% emerging between 2100 and 2200 hr (Callahan 1958). None emerged after midnight.

Little information has been published concerning armyworm, *Pseudoletia unipuncta* (Haworth), emergence. Hundreds of armyworms were observed in the field emerging after a rain shower (Knight 1916). Sunshine was noted to produce greater moth emergence. In a laboratory colony of pale western cutworm, *Agrotis orthogonia* Morrison, 90.7% of both sexes emerged between noon and midnight (Jacobson 1965). Nearly one half emerged between 1400 and 1600 hr. Under laboratory conditions, 93% of black cutworm, *Agrotis ipsilon* (Hufnagel), emerged between sunset and sunrise (Nasr and Naguib 1963). Most emergence occurred between 2000 and 0400 hr with a peak at 2200 hr.

The objectives of the noctuid adult eclosion research presented in this paper were to examine the cycle as well as the daily rhythm of black
cutworm and armyworm emergence. Further, the study examined the differences that existed between populations held for approximately 6 and 18 generations in the laboratory. Variations in adult emergence could have consequences for flight takeoff and moth survival. The final aspect of the study was to examine differences in the diel periodicity of colonies when held in cold storage (15.5°C) for 1 wk as compared with standard rearing temperatures. Cold storage is commonly used to delay emergence for studies of long-range movement of adults using mark-release-recapture techniques and studies for assessment of larval damage to corn.
MATERIALS AND METHODS

The armyworm and black cutworm used in the experiment were from laboratory colonies. The 1987 colonies for both species were collected from eggs laid by adults captured during the summer of 1987 and were approximately 18 generations removed from feral populations when experimentation commenced. The 1988 colonies were collected in a like manner and were approximately six generations removed from the wild when experimentation commenced. Under colony maintenance rearing procedures, adults and pupae were held in L:D of 14:10 with lights off at 2000 hr CST. The temperature was held at 24°C ± 2° during the day and 21°C ± 2° during the night. Larvae were held in rearing rooms with 24 hr light and 27°C ± 2°. However, the larvae were exposed to little direct light because of the opaque walls of the individual rearing containers. Humidity for all rearing was approximately 75%.

Two additional treatments were tested. First, standard colony rearing temperatures and cold storage were compared. Pupae subjected to cold storage facilities were held at 15.5°C ± 1°, 24 hr light, and 75% RH for one week. Cages were constructed of 9880 cc plastic tubing. Pupae were covered with moist vermiculite (Terra-Lite #2, Grace Horticultural Products, Cambridge, Mass) to prevent desiccation. As each treatment's pupae were harvested, counts were made and the pupae evenly divided among 10 cages. The armyworm pupae held in cold storage were placed 75 per cage and the black cutworm pupae were placed 150 per cage. The armyworm
pupae reared under standard temperatures also were divided into 75 pupae per cage. Black cutworm pupae reared under standard conditions were placed 120 per cage. Black cutworm emergence cages were randomly placed on the top shelf in the environment chamber and armyworm cages placed on the second shelf. Cages were rotated within shelves daily until emergence began and rotated hourly thereafter.

The experimental design was 23 factorial with two species, two colonies per species and two temperature treatments of each colony. After the first moth emergence, collections were made hourly. Moths collected were placed into 568 cc plastic bags. Treatments were recorded and samples were frozen. Moths were subsequently unfrozen, counted and sexed. To condense the data, statistical analysis was done after grouping observations into 4 hr time periods. Chi-square statistics (SAS Institute 1985) were then calculated to evaluate differences in emergence over time between the two temperatures, between the two populations and between the two species. Statistics could not be used on the population cycles because replications were based on daily cycles.
RESULTS

In total, 8839 moths were examined. Both black cutworm and armyworm emerged over a 10-day period. For black cutworm, the 1987 standard temperature and the 1987 cold storage treatments produced similar emergence cycles (Figure 1). Both emerged earlier than did the 1988 colony within either treatment. Differences in sex were not noticeable in the emergence cycle. For both standard temperature and cold storage, emergence of the two sexes was related to time the colony was kept under laboratory conditions (Figures 2, 3).

The effects of temperature treatment were different for the two species. Both colonies of armyworm under the standard temperature treatment emerged quicker than the pupae held in cold storage (Figure 4). This finding would indicate that the armyworm must overcome some inhibitory effect of cold storage that the black cutworm does not. Sex effects were not pronounced in the standard temperature treatment (Figure 5). In the cold storage treatment, the 1988 colony females seemed to emerge earlier than did the males (Figure 6).

The daily differences between the 1987 colonies of the two species, significant differences were found using the chi-square analysis ($X^2 = 231.17; df = 5; P = 0.000$). Large variation was present in every time period. Significant differences also were observed between the 1988 colonies of the two species ($X^2 = 206.59; df = 5; P = 0.000$). Large variations were found in every time period except 0900 hr.
Figure 1. Chronological sequence of the black cutworm emergence cycle shown by day. Observations were pooled over hour and sex to emphasize temperature treatments.
No. of Moths

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- Standard temp, 1988
- Cold storage, 1988
Figure 2. Emergence cycle of black cutworm subjected to standard rearing temperatures shown by day. Observations were pooled over hour and shown as daily emergence.
No. of Moths

Day

No. of Moths

Day

- Female 1988
- Male 1988
- Female 1987
- Male 1987
Figure 3. Black cutworm emergence after cold storage. Results shown by day and with observations pooled over hour.
No. of Moths

Day

0  10  20  30  40  50  60  70  80  90  100

Female 1988  Male 1988  Female 1987  Male 1987
Figure 4. Chronological sequence of armyworm emergence cycle shown by day. Observations were pooled over hour and sex to emphasize temperature treatments.
No. of Moths

Day

- - Standard temp, 1988
- - Cold storage, 1988
- - Standard temp, 1987
- - Cold storage, 1987
Figure 5. Emergence of armyworm under standard rearing procedure shown by day. Hourly observations were pooled and shown as daily emergence.
No. of Moths

Day

Female 1988
Male 1988
Female 1987
Male 1987
Figure 6. Daily armyworm emergence of moths subjected to cold storage. Observations were pooled over hour.
No. of Moths

Day

Female 1988 Male 1988

35
30
25
20
15
10
5
0

1 2 3 4 5 6 7 8 9 10

Female 1988 Male 1988 Female 1987 Male 1987
There were also significant differences between the two black cutworm colonies with all other treatments combined ($X^2 = 15.74; df = 5; P = 0.008$). Chi-square analysis showed that the greatest variation occurred at 1400 hr when the 1987 colony eclosion was proportionally larger. Likewise, significant differences were found when comparing the colony differences for armyworm ($X^2 = 21.96; df = 5; P = 0.001$). The largest variations occurred during 1000 and 1400 hr periods when proportionally more of the 1987 armyworm colony emerged. Daily emergence differences of the colonies of the two species are presented in Figure 7.

A significant difference between the two black cutworm colonies reared at standard temperatures ($X^2 = 21.335; df = 5; P = 0.001$) was found. The 1987 colony showed a larger deviation from the average in the 0200 hr period, while the 1988 colony had a greater number emerge at 1800 hr (Figure 8). It would seem, therefore, that under standard rearing temperatures the 1988 colony began emergence earlier than the 1987 colony. In both colonies, however, the daily peak emergence time was 2200 hr with 42.7% of the 1987 colony and 44.4% of the 1988 colony emerging. In the 1987 colony, 78.3% emerged during the 2200 and 0200 periods. Likewise, 71.1% of the 1988 colony emerged during these same time periods. The two black cutworm colonies in cold storage were significantly different ($X^2 = 59.598; df = 5; P = 0.000$). Chi-square analysis showed the largest deviation occurred between 0200, 1400 and 1800 hr periods with the 1987 colony emergence higher in all three (Figure 8). Again, the daily peak emergence was 2200 hr with 40.3% of
Figure 7. Daily emergence of black cutworm and armyworm to show colony differences. Observations were combined into four hour periods.
No. of Moths

1988 black cutworm
1988 armyworm
1987 black cutworm
1987 armyworm

Time
Figure 8. Daily emergence of black cutworm under standard or cold rearing procedures. Observations were combined into four hour periods.
No. of Moths

<table>
<thead>
<tr>
<th></th>
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<tbody>
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<td>1800</td>
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</tr>
<tr>
<td>3000</td>
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</tbody>
</table>
Figure 9. Daily periodicity of armyworm emergence held in standard or cold storage. Observations were made hourly and combined into four hour periods.
No. of Moths

Time

1400 1800 2200 200 500 900

- Standard 1988 AW
- Standard 1987 AW
- Cold 1988 Armyworm
- Cold 1987 Armyworm
the 1987 colony and 38.5% of the 1988 colony emerged during these periods. The 2200 and 0200 hr periods combined encompassed the bulk of emergence with 63.0% and 74.5% for the 1987 and 1988 colonies, respectively.

The armyworm colonies under standard rearing temperatures showed significant differences ($X^2 = 33.122; df = 5; P = 0.000$) in emergence times. The major differences occurred at 1000 and 1400 hr. In both hourly periods, the 1987 colony had a larger number of moths emerging than did the 1988 colony (Figure 9). Under the cold storage conditions there were no significant differences ($X^2 = 2.770; df = 5; P = 0.735$) between colonies over time (Figure 9). Peak emergence for both colonies under standard temperatures was 2200 hr with 22.8% of the 1987 colony and 42.3% of the 1988 colony emerging. During 1800 and 2200 hr, 42.2% of the 1987 colony emerged and 62.4% of the 1988 colony. Cold storage affected armyworm moths as follows; 25.6% of the 1987 colony emerged and 29.8% of the 1988 colony emerged during 200 hr. Moth emergence of the 1987 colony achieved 47.2% while 49.0% of the 1988 colony emerged during 1800 and 2200 hr.

There were no significant differences between sexes in the 1987 and 1988 black cutworm colonies held at standard temperatures ($X^2 = 2.847; df = 5; P = 0.724$ and $X^2 = 7.603; df = 5; P = 0.180$, respectively) (Figure 10). However, there were significant differences in the 1987 cold storage black cutworm colonies ($X^2 = 14.952; df = 5; P = 0.011$). The greatest contribution for sex differences came during the 0600 and 1800
Figure 10. Daily emergence of male and female black cutworm subjected to standard rearing temperatures. Hourly observations were combined into four hour periods.
Figure 11. Diel emergence of male and female black cutworm held in cold storage. Hourly observations were combined into four hour periods.
No. of Moths

Time

Females emerged in larger numbers in the former time period while more males emerged in the latter (Figure 11). Significant differences also were observed in the 1988 colony ($X^2 = 17.332$, df = 5; $P = 0.004$). The major differences were during the 0200 hr and 1800 hr periods. Females emerged in larger proportion with the males in the former time period (Figure 11). It would seem, therefore, that females held in cold storage emerge in larger numbers after midnight than do males that have been held in cold storage. Males emerge in comparatively larger numbers, however, with the onset of the dark phase.

There were no significant differences between the sexes of armyworm from the standard temperature 1987 colony ($X^2 = 5.801$, df = 5; $P = 0.326$) (Figure 12). Likewise, the 1987 colony of armyworms held cold storage showed no significant differences ($X^2 = 1.910$, df = 5; $P = 0.861$) (Figure 13). There was no significant difference between the 1988 colony under standard rearing procedure for sex ($X^2 = 5.336$, df = 5; $P = 0.376$) (Figure 12) or the 1988 colony under cold storage for sex ($X^2 = 3.560$, df = 5; $P = 0.614$) (Figure 13).
Figure 12. Diel emergence of male and female armyworm reared with standard rearing temperatures. Hourly observations were combined into four hour periods.
Figure 13. Diel emergence of male and female armyworm held in cold storage for one week. Hourly observations were combined into four hour periods.
DISCUSSION

Overall, the emergence cycle was affected by the cold storage treatment. Armyworm was affected more by the cold storage than black cutworm. Pupal emergence was inhibited, regardless of the colony age. Conversely, the black cutworm colony shows a laboratory rearing effect, with the older colony being selected for earlier emergence. Under current rearing techniques, the black cutworm colonies normally reproduce well. Therefore, fewer individuals are needed to maintain the colony and satisfactory numbers are obtained from larvae which pupate early. Larvae which pupate later are not introduced into colonies, whereas later pupating larvae are needed for the more difficult to rear armyworm colonies. This procedure might select for earlier emergence among black cutworms. It is important to note, however, that the length of the emergence cycle is the same for both colonies.

Sex effects during the emergence cycle between the colonies were small. No differences were observed in the emergence cycle of either species. These results for the emergence cycle contradict the findings of Lingren et al. (1988) where female corn earworms emerged in greater numbers during the emergence cycle. These results are also contrary to the results by Gaines (1933). He found male corn earworms to be more common during the first week of each generation.

Daily emergence cycles showed differences between colonies. Although both species had peak emergence at 2200 hr, the armyworm began emergence sooner after onset of darkness. The bulk of black cutworm eclosion was
skewed to the 2200 and 0200 hr periods. These findings contradict the suggestion by Knight (1916) that armyworm emergence was common during the day. These results also differ from Jacobson (1965) where nearly one-half of the pale western cutworm emergence was found to occur between 1400 and 1600 hr. Daily emergence patterns found in this study complement published work (Quaintance and Brues 1905, Callahan 1958, Hardwick 1965, Lingren et al. 1988) for the corn earworm where peak emergence in both the field and laboratory was often found to be between 2200 and 2400 hr. Published work on laboratory reared black cutworm show emergence between 2000 and 0400 hr with a peak at 2200 hr (Nasr and Naguib 1963), a finding these results support.

Effects of cold storage on the colonies was evident. The 1987 black cutworm colony was most strongly affected, with a weakening of the emergence peak. The emergence of the 1987 armyworm colony under standard rearing temperature spreads the emergence times from the peak time period. Cold storage of this colony negated the sharp emergence peak seen after cold storage of the 1988 armyworm colony.

Cold storage affected emergence between the sexes of black cutworm. The males emerged in higher proportion to the females at the onset of dark. The females emerged more strongly later in the evening, showing a second peak at 0600 hr. The influence of cold storage on the emergence periodicity, although statistically significant in many instances, did not seem to cause major behavioral shifts for the two species. Cold storage, therefore, offers a practical method of controlling time of emergence for these two species.
A review of the literature found that most nocturnal moths emerge in the afternoon and/or early evening (see Dreisig 1986) and the insects cited often mated the first night posteclosion. It was not uncommon, because of sexual competition, for the male to emerge first. However, in a number of species the females do not start calling until several days after eclosion and it was not known if the species with delayed sexual maturity have a different pattern of diel emergence than other species (Dreisig 1986). The corn earworm mates on the night after eclosion, but not on the night of eclosion (Callahan 1958, Lingren et al. 1988). No sexual differences were found on nightly emergence in the field (Lingren et al. 1988). The armyworm does not call on the day following emergence and generally begins to call several days after emergence (Turgeon and McNeil 1982, 1983). Just 20% of black cutworm females began to call after 1 day, with 4-day-old females calling most frequently (Swier et al. 1977, Kaster et al. 1989 and Mulder et al. 1989). This calling behavior corresponded to sexual maturity of the moth (Swier et al. 1977). Both of the insect species used in this study become sexually mature several days posteclosion and sex emergence differences were not found under standard rearing temperature. This finding indicates emergence of noctuid species that become sexually active after several days does not exhibit the early emergence of the male.
PART II. POSTECLOSION FEEDING OF LABORATORY REARED
ADULT ARMYWORM, *PSEUDALETIA UNIPUNCTA* (HAWORTH), AND BLACK CUTWORM,
*AGROTIS IPSILON* (HUFNAGEL) (LEPIDOPTERA: NOCTUIDAE)
INTRODUCTION

The daily onset of a nocturnal feeding flight is very important in synchronizing the insect with the plant’s nectar flow. Studies on the periodicity of adult feeding behavior, however, have been reported infrequently. Cabbage looper, *Trichoplusia ni* (Hübner), activity was found to began about 30 min before sunset (Shorey et al. 1962) while the tobacco budworm, *Heliothis virescens* (F.), adult feeds between 1900 and 2000 hr (AST) (Lingren et al. 1979). Peak feeding activity for female tobacco budworms, however, occurred about 1 hr later than that of males. A separate study found tobacco budworm and cabbage looper both began their feeding activity at 2000 hr (Lingren et al. 1977). *Heliothis armigera* (L.) began feeding at 1815 hr (GMT + 2 hr) and peaked between 1815 and 1930 hr (Topper 1987). After 1930 hr, activity decreased almost linearly. Corn earworm, *Heliothis zea* (Boddie), feeding on sorghum and corn, began activity at dusk, decreasing until cessation at 2400 hr (Roome 1975).

These reports, however, do not provide answers for the timing of first feeding in recently emerged moths. Feeding postemergence is especially critical because it provides needed energy for migration and oviposition. Female corn earworm nectar feeding has been shown to produce a large complement of eggs (Nuttycombe 1930). Newly emerged corn earworm moths were observed feeding on corn exudates before their wings were expanded (between 11 and 69 min after emergence) (Lingren et al.)
Further, the European corn borer, *Ostrinia nubilalis* (Hübner), female fed honey-water increased egg weight (Miller 1988).

Female cabbage loopers were found to feed an average of 2.2 times on the night following their emergence (Shorey et al. 1962). On the second night, they fed an average of 3.0 times. Males also fed frequently but were not discussed in detail by the researchers. Laboratory-reared corn earworm imagoes were observed to visit feeders at least once on the emergence night, feeding from 1 to 3 minutes (Callahan 1958).

The purpose of this study was to investigate the posteclosion feeding in laboratory colonies of armyworm, *Pseudaletia unipuncta* (Haworth), and black cutworm, *Agrotis ipsilon* (Hufnagel). Sexual differences were also examined. Finally, feeding differences between normal moths with wings fully expanded and deformed moths with wings incompletely expanded were analyzed. Incompletely expanded wings also denotes extremely recent emergence.
MATERIALS AND METHODS

Black cutworm and armyworm used in these experiments were six to eight generations removed from the wild. Moths and pupae were held in L:D of 14:10 with lights off at 2000 hr GST. The temperature was held at 24°C ± 2° during the day and 21°C ± 2° during the night. Humidity was approximately 75%. One hundred fifty pupae were placed into 12 separate 9880 cc plastic emergence cages. Pupae were then covered with moist vermiculite (Terra-Lite #2, Grace Horticultural Products, Cambridge Mass.) to prevent desiccation. Black cutworm emergence cages were randomly placed on the top shelf in the environment chamber and armyworm cages placed on the second shelf. Cages were rotated daily within shelves. The first three nights of emergence were not sampled to allow for population emergence to reach sufficient numbers.

Beginning at 2000 hr, all moths were removed from cages so moths used for the experiment would be less than 1 hr old. Night vision goggles (Litton Electric Tube Division, Tempe, Ariz.) that allow the observer to see without overhead lighting were used to prevent disturbing the moths. Moths were gently vacuumed up at hourly intervals and placed into 9880 cc cages equipped with a 36 cc black plastic film container filled with absorbent cotton (Red Cross Cotton, Johnson and Johnson Product Inc. New Brunswick, NJ). The food was a modification of the Reese et al. (1972) adult diet with 15 ml water soluble florescent dye (540 Red, #1962, Liquitex Florescent Poster Colors, Binney and Smith Inc., Easton, Penn.)
added per 184 cc adult diet and was presented through holes drilled in the containers.

Two complete replications for each species were made. The experimental design was a 4x4 Latin square controlling for time of emergence within night and number of nights. From previous observations, peak emergence occurred between 2100 and 2400 hr CST. For this reason, collections were begun at 2100 hr and at hourly intervals thereafter until 2400 hr. Treatments were 1, 2, 4 and 6 hr feeding postemergence. The four treatments were assigned to a particular time of emergence during the night. This was rotated nightly so that each treatment occurred once per square during each emergence time.

Moths were held in total darkness and allowed to feed. At the end of the treatment time, moths were frozen. Subsequently, moths were unfrozen and sorted by sex and wing development. Moths with fully expanded wings were recorded as normal, while those with incompletely expanded wing were termed deformed. Newly emerged moths that were deformed remained so because of the disturbance during the collection technique. Therefore, species, sex and wing development were analyzed to determine the impact of these conditions on feeding postemergence. Percent moths in each category were transformed by arcsine/σ and analyzed with ANOVA (SAS Institute 1985). Duncan’s multiple range test (Duncan 1955) was used to separate significant differences in treatment means (P ≤ 0.05).
RESULTS AND DISCUSSION

Significant differences were not evident for feeding between the two species by normal moths ($F = 1.31; \, df = 1, \, 180; \, P = 0.1251$) but there were differences in feeding between the species for deformed moths ($F = 34.00; \, df = 1,58; \, P = 0.0001$). The deformed black cutworm fed proportionally more than the deformed armyworm (Table 4). There were also significant differences between the deformed and normal moth when feeding of the two species were combined ($F = 113.65; \, df = 1, \, 180; \, P = 0.0001$). As might be expected, a greater percentage of the normal moths fed than did the deformed (Table 5) with the deformed armyworm moths (arcsine mean = 0.41) feeding less than the deformed black cutworm (arcsine mean = 0.92). Between species, treatments were not significantly different ($F = 2.58; \, 3, \, 180; \, P = 0.0552$) for moth feeding.

There was a significant difference between replications for black cutworm ($F = 17.66; \, df = 6, \, 74; \, P = 0.0001$). There was a trend for these differences (Table 6), nights one and two, and nights five, six, respectively, were the first two nights within the two replications of the Latin square. These nights might differ because of human error; the recorder becomes more sensitive to the presence of the dye and records moths feeding on subsequent nights that would be missed during the first nights. Significant differences were found between replications ($F = 2.74; \, df = 6, \, 106; \, P = 0.0163$) of armyworm as well. Trends, however, could not be found for nightly replications (Table 6).
Differences were not significant between times black cutworm feeding began ($F = 1.76; \text{df} = 3, 74; P = 0.1630$). There was a feeding difference between time of night ($F = 3.15; \text{df} = 3, 106; P = 0.0281$) for armyworm, however. The moths collected at 0200 and 2100 hr (arcsine means = 0.91 and 0.72, respectively) fed in larger numbers than those at 2400 and 1900 hr (0.69 and 0.62, respectively) (Table 7).

Table 4. Mean separation of feeding by species shown as arcsine transformation of percent feeding by deformed moths$^1$

<table>
<thead>
<tr>
<th>Colony</th>
<th>Arcsine Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black cutworm</td>
<td>0.92 a</td>
</tr>
<tr>
<td>Armyworm</td>
<td>0.41 b</td>
</tr>
</tbody>
</table>

$^1$Means followed by the same letter are not significantly different ($P > 0.05$) by Duncan's multiple range test (Duncan 1955).
Table 5. Feeding of deformed moths and normal, moths combined over species. Results are presented as arcsine transformation of percent feeding by moth feeding.\(^1\)

<table>
<thead>
<tr>
<th>Wing Development</th>
<th>Arcsine Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Normal</td>
<td>1.05 a</td>
</tr>
<tr>
<td>Deformed</td>
<td>0.58 b</td>
</tr>
</tbody>
</table>

\(^1\)Means followed by the same letter are not significantly different \((P > 0.05)\) by Duncan's multiple range test (Duncan 1955).
Table 6. Mean separation of nightly replication for black cutworm and armyworm. Results shown as arcsine transformations of the mean percent of feeding moths.

<table>
<thead>
<tr>
<th>Black cutworm</th>
<th>Arcsine Mean</th>
<th>Armyworm</th>
<th>Arcsine Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Replication</td>
<td></td>
<td>Replication</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>1.21 a</td>
<td>4</td>
<td>0.88 a</td>
</tr>
<tr>
<td>4</td>
<td>1.21 a</td>
<td>6</td>
<td>0.88 a</td>
</tr>
<tr>
<td>7</td>
<td>1.17 ab</td>
<td>7</td>
<td>0.86 a</td>
</tr>
<tr>
<td>8</td>
<td>1.01 bc</td>
<td>5</td>
<td>0.84 a</td>
</tr>
<tr>
<td>2</td>
<td>1.01 bc</td>
<td>1</td>
<td>0.77 ab</td>
</tr>
<tr>
<td>6</td>
<td>0.93 c</td>
<td>3</td>
<td>0.57 ab</td>
</tr>
<tr>
<td>5</td>
<td>0.74 d</td>
<td>8</td>
<td>0.54 b</td>
</tr>
<tr>
<td>1</td>
<td>0.69 d</td>
<td>2</td>
<td>0.53 b</td>
</tr>
</tbody>
</table>

Means followed by the same letter are not significantly different \( (P > 0.05) \) by Duncan's multiple range test (Duncan 1955).
Table 7. Comparison between time of emergence and feeding for armyworm (CST). Results shown as arcsine transformations of mean percent

<table>
<thead>
<tr>
<th>Time</th>
<th>Arcsine Mean</th>
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</thead>
<tbody>
<tr>
<td>2200</td>
<td>0.91 a</td>
</tr>
<tr>
<td>2300</td>
<td>0.72 ab</td>
</tr>
<tr>
<td>2400</td>
<td>0.69 b</td>
</tr>
<tr>
<td>2100</td>
<td>0.62 b</td>
</tr>
</tbody>
</table>

Means followed by the same letter are not significantly different (P > 0.05) by Duncan's multiple range test (Duncan 1955).

Both sexes of the two species were attracted to the food source in comparable numbers. Sex differences were insignificant for black cutworm (F = 0.01; df = 1, 74; P = 0.9320) and also armyworm (F = 2.44; df 1, 106; P = 0.1210).

The amount of feeding between normal winged and deformed winged black cutworm was significantly different (F= 23.93; df 1, 74; P = 0.0001) with more normal winged individuals feeding compared with deformed individuals (arcsine mean = 1.05 and 0.92, respectively). Deformed armyworm moths (arcsine mean = 0.41) were significantly less likely to feed than their normal (arcsine mean = 1.05) counterparts (F = 83.50; df = 1, 106; P =
Because of the locations of the feeding stations, deformed moths might have had less access to the food source. Feeding canisters were suspended from the top of the cage and the cage sides would have been difficult for moths to climb. Normal moths could fly easily to the stations. Deformed moths were often observed feeding on the bottom of the cages, where excess food had dripped. These findings were similar to those of Lingren et al. (1988) where corn earworm moths were found to have fed before the wings were fully expanded.

Significant differences were also found between feeding times ($F = 6.38; \text{df} = 3, 74; P = 0.0007$) for normal black cutworm. As expected, the longer moths were exposed to food, the greater the numbers that fed (Table 8). But, by the end of the first hour 71.3% had fed. Unlike the black cutworm, however, differences between feeding times for armyworm were not found ($F = 1.20; \text{df} = 3, 106; P = 0.3132$). Again, however, by the end of the first hour 71.6% had fed.

Over 70% of both species of these important noctuids fed in the laboratory within 1 hour after eclosion, and nearly 87% fed within 6 hours. Even deformed moths, without expanded wings take food. Obviously, this is an important behavioral component for newly emerged adults. The laboratory results for armyworm and black cutworm corroborate field observations of newly emerged corn earworm found feeding extensively on corn stubble (Lingren et al. 1988). Manipulation of this behavior might conceivably be used for pest management. Poison baits or trap crops could be used for reducing newly emerged populations (Lingren et al. 1988). The attractiveness of food baits for adults has
been proven by Rose et al. (1985). They marked natural populations of African armyworm, *Spodoptera exempta* (Wlk.), with dyed molasses painted onto trees near the emergence site. In all, 166,000 moths were estimated to have been marked.

Table 8. Feeding by normal black cutworm moths over time. Results presented as arcsine transformation of mean percent of feeding moths

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Arcsine</th>
<th>Times (hr)</th>
<th>Means</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>1.11 a</td>
<td>1.11 a</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>1.04 ab</td>
<td>1.04 ab</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>0.98 bc</td>
<td>0.98 bc</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.89 c</td>
<td>0.89 c</td>
<td></td>
</tr>
</tbody>
</table>

\(^1\)Means followed by the same letter are not significantly different (P > 0.05) by Duncan's multiple range test (Duncan 1955).

Feeding activity is also critical for migration. Migrant moths that fed previously and were reproductively mature could oviposit upon arrival.
without further feeding. Furthermore, manipulation of feeding sites in the source area offers a potential method for control of migrating populations (Lingren et al. 1988). The results from this research show that a large majority of black cutworm and armyworm feed if food sources are available. Further knowledge of attractive plant hosts for adult feeding is needed to test these potential control methods.
PART III. NOCTURNAL FEEDING BEHAVIOR OF COMMON ADULT MOTHS IN IOWA
Field observation is one of the most useful methods of recording feeding activity of important nocturnal moths. A review of the general feeding habits of moths feeding on nectar, sap, water and animal excreta has been compiled by Norris (1936). Further, a comprehensive study of moth feeding was compiled from common plants in Illinois (Robertson 1929). Tests of feeding activity with *Autographa gamma* in Europe have been done as well (Schremmer 1941). The first *Autographa gamma* moths always appeared at dusk and flight activity began earlier as the daylengths shortened. Moths were seen on *Scabiosa ochroleuca*, *Melandryum album*, *Silene vulgaris*, *Dianthus* sp. and *Trifolium* sp. Twenty species of Plusiinae (Noctuidae), including *Autographa precationis*, were collected from hosts in northern Michigan (Nielsen 1981). The host plants from which insects were collected were *Asclepias syriaca*, *Apocynum androsaemifolium*, *Centaurea maculosa*, *Epilobium angustifolium*, *Cirsium* sp., *Diervill lonicera*, and *Eupatorium* sp.

Observations have also been made on nocturnal insects feeding on cotton (*Gossypium hirsutum* L.). In California, cabbage loopers, *Trichoplusia ni* (Hübner), were observed feeding on spiny aster, *Aster spinosus* (Benth.), and cotton (Shorey et al. 1962). Moth activity began about 30 min before sunset. Tobacco budworm, *Heliothis virescens* (Fabr.), adults in Puerto Rico and St. Croix began feeding between 1900 and 2000 hr, (AST) (Lingren et al. 1979). Peak feeding activity for females occurred about 1 hr later than that of males. Feeding activity
was observed until 0300 to 0400 hr. Cabbage looper and soybean looper, *Pseudoplusia includens* (Walker), were active in large numbers in cotton and soybean (*Glycine max* L.) fields in Alabama (Lingren et al. 1979). Similarly, soybean loopers in Louisiana were found feeding on cotton nectar (Jensen et al. 1974). The cotton leaf perforator, *Buccalatrix thurberiella* (Busck.), fed extensively on cotton during the night (Lingren et al. 1980). Feeding activity began near dusk, peaked shortly thereafter, and then declined. The tobacco budworm, *Heliothis virescens* (F.), and cabbage looper were also found feeding on tobacco and careless weed (*Amaranthus spinosus*) (Lingren et al. 1977). Both species began their activity at 2000 hr.

The corn earworm, *Heliothis zea* (Boddie), because of its economic importance, has been studied more extensively than most moths. An extensive feeding list of attractive plants for the corn earworm has been compiled from both captive studies and from nature (Nuttymcombe 1930). Large numbers of corn earworm were observed congregating in blooming soybean fields (Barber 1938). This insect has been observed feeding on tobacco (*Nicotiana tabacum*), bush bean (*Phaseolus vulgaris*), *Petunia* (*Petunia* spp.), hog peanut (*Amphicarpaea bracteata*), jimsonweed (*Datura stramonium*), morning glory (*Ipomoea purpurea*), puncture vine (*Tribulus terrestris*) (Callahan 1958), sweet clover (*Melilotus sp.*) (Garman and Jewett 1914), lima bean (*Phaseolus limensis*) (Pepper 1943) and the nectaries of cotton (Fletcher 1929 and Gaines 1933).

Corn earworm has also been found feeding on cotton, Joepye weed (*Eupatorium purpureum*), plum (*Prunus americana*), sunflower (*Helianthus*
sp.) and buffalo bur (Solanum rostratum) (Quaintance and Brues 1905). Feeding usually began after 1800 or 1900 hr, but if food was scarce, feeding began earlier. Observations on corn earworm in Arkansas found feeding usually began between 1630 and 1700 hr (CDT) and the moths fed on crimson clover (Trifolium incarnatum L.), white clover (Trifolium repens L.), sweet clover (Melilotus sp.), alfalfa (Medicago sativa L.), evening primrose (Oenothera sp.), and cotton (Phillips and Whitcomb 1962). Ryegrass (Lolium perenne L.) and Dallis grass (Paspalum dilatatum Poir.) were also attractive because of the exudate produced by Claviceps purpurea (Fr.). In Botswana, corn earworm began feeding on sorghum (Sorghum spp.) and corn (Zea mays L.) at dusk with activity decreasing until 2400 hr (Roome 1975). Feeding on pigeonpea (Cajanus cajan) nectar was heaviest before and during sunset (Adler 1987). Newly-emerged corn earworm moths fed on corn exudates even before their wings were expanded (between 11 and 69 min after emergence) (Lingren et al. 1988).

Armyworm, Pseudaletia unipuncta (Haworth), were observed feeding on mashed and decaying apples and also on nectar of catnip, Nepeta cataria (L.) (Knight 1916). With black cutworm, many winter annual weeds and perennial trees bloom very early in the midwest and may be attractive for feeding and oviposition (Sherrod 1976). Feeding records of black cutworm, Agrotis ipsilon (Hufnagel), were collected in Missouri from late April to October between the hours of 2230 and 0400 (CST) (Wynne and Keaster 1987). Attractive plants were: wild plum (Prunus americana Marsh), crabapple (Malus sp.), common lilac (Syringa vulgaris L.), autumn olive (Elaeagnus umbellata Thunb.), wild cherry (Prunus serotina Ehrh.),
amur maple (*Acer ginnala*), Russian olive (*Elaeagnus angustifolium* L.),
black locust (*Robinia pseudoacacia* L.), linden (*Tilia* spp.), privet
(*Ligustrum ovalifolium* Hassk.), northern catalpa (*Catalpa speciosa*
Warder), goldenrain tree (*koelreutaria paniculata*), red clover (*Trifolium*
*pratense* L.) and common milkweed (*Asclepias syriaca* L). The flowers of
linden were especially attractive. Further, all of the plants attractive
to black cutworm were also attractive to armyworm.

Several reports have focused entirely on milkweed pollinators.
Several *Autographa precationis* (Gn.) were found hanging dead by their
proboscis or maxillae, caught by the pollen "trap" of an asclepiad
(Packard 1880). Nectar was produced mainly by *Asclepias verticillata* L.
between 1800 and 2200 hr, making it attractive to many night feeders
(Willson et al. 1979). Similarly, in Illinois, maximum sugar content in
*Asclepias syriaca* was at 2200 hr (Willson and Bertin 1979). Noctuidae
comprised 39-52% of the native pollinators. The variegated cutworm,
*Peridroma saucia* (Hübner) and the black cutworm were often the most
important pollinators. The armyworm and *Leucania multilinea* were common
feeders during part of the study. Moths were also commonly found on *A.*
*verticillata* (Willson and Bertin 1979). The black cutworm and *Autographa*
*precationis* were occasionally captured on this species.

Pollen carried on moths can be used as an indicator of flower
visitation. Most research on pollen loads has centered on butterflies
(e.g., Poulton 1929, Higston 1929, Wiklund et al. 1979, Grace and Nelson
1981, Courtney et al. 1982 and Lazri and Barrows 1984). In a
palynological analysis of pollination by hawk moths, 13 different plant
species were identified from pollens and the flowers fell into two groups, those that are pollinated exclusively by the proboscis and those that are pollinated by other body parts as well (Kislev et al. 1972). Pollen on 68.3% of the corn earworms examined in Arkansas (Hendrix et al. 1987). Most of the pollen was on the proboscis (87%) or on the eye (11.8%).

The purpose of this research was to study the nocturnal feeding behavior of moths in Iowa. Insects were observed while feeding and then collected. Data on sex ratios, ovipositional development, and pollen distribution were used to determine seasonal and hourly trends of feeding.
MATERIALS AND METHODS

Collections were made over a 4 year period from May through September. Weather permitting, collections were made at least twice a week and began at dusk with two to four observers. Moths were observed feeding, then collected and placed into 21 ml cups (#P075S, Plastic Souffles, Solo Cup Co., Urbana, IL). Collection of moths was made with a sweep net or by hand. The moth thorax was crushed before placing into the cups to prevent wing damage. Time of collection (in 15 min intervals), plant type and date were recorded on each cup. Collections continued until feeding observations fell below two per observer per time period. Collections were not made in the rain. All observations were made near the USDA-ARS Corn Insects Research Laboratory on the Iowa State University Research Farm, Ankeny, IA.

Insects were collected from: common milkweed, *Asclepias syriaca* (L.) (Asclepidaceae); whorled milkweed, *Asclepias verticillata* (L.) (Asclepidaceae); sweet clover, *Melilotus officinalis* (L.) and *Melilotus albus* (Desr.) (Leguminosae); red clover, *Trifolium pratense* (L.) (Leguminosae); white campion, *Lychnis alba* (Mill.) (Caryophyllaceae); brome grass, *Bromus* spp. (Gramineae); wild carrot, *Daucus carota* (L.) (Umbelliferae); alfalfa, *Medicago sativa* (L.) (Leguminosae); bull thistle, *Cirsium vulgare* (Savi) (Compositae); Indian hemp, *Apocynum cannabinum* (L.) (Apocynaceae); tall joepye weed, *Eupatorium altissimum* (L.) (Compositae); goldenrod, *Solidago* sp. (Compositae); smartweed, *Polygonum* sp.; common lilac, *Syringa vulgaris* (L.) (Oleaceae); and honeysuckle, *Lonicera morrowi* (Gray.) (Caprifoliaceae).
At the end of each nightly collection, moths were frozen. Subsequently, species, sex and mated condition of females were recorded. Reproductive condition of the females was based on the Showers et al. (1974) classification. Class I females were unmated, class II females contained full spermatophores and were gravid, class III females were partially depleted of eggs and class IV females were completely depleted of eggs.

Moths were examined with a microscope under 100x magnification for pollen and milkweed pollinia. Data were combined so that 15-minute intervals were equivalent from dusk. This would generate a base time throughout the season and remove seasonal effects created by widely changing time of dusk. Seasonal cycles were combined for the four years to simulate 17 wk of observation.
RESULTS

Moth Feeding Activity

A total of 2296 moths were collected from May through September over a 4 year period. In 1986, common milkweed was sampled a total of 19.25 hr over 10 nights, whorled milkweed 16.25 hr over eight nights, brome grass once for 2.0 hr, red clover on six occasions for 10.25 hr, white campion 5.0 hours over six nights, and alfalfa 5.5 hr over four nights. In 1987, common milkweed was sampled 8.0 hr over six nights, red clover 6.5 hr over three nights, sweet clover 4.25 hr over three nights, wild carrot 4.25 hr over three nights, brome grass was sampled 6.5 hr over 5 nights, bull thistle 2.45 hr over two nights and alfalfa 13.25 hr over seven nights. In 1988, milkweed was sampled 4.25 hr over three nights, sweet clover was sampled once for 0.5 hr, brome grass 3.5 hr over two nights, alfalfa 20.25 hr over nine nights, Indian hemp 5.25 hr over two nights, smartweed 2.75 hr over two nights, goldenrod 8.75 hr over 5 nights and tall joepye 2.75 hr over two nights. In 1989, lilac was sampled 2.75 hr over two nights and honeysuckle 3 hr over two nights.

The moths collected comprised 36 species, representing the families Noctuidae (28 species), Pyralidae (4 species), Arctiidae (2 species) and Geometridae (2 species) (Table 9). A summary of the collections and respective sex ratios shows that of the 36 species, only 19 were collected in sufficient numbers (>10) to warrant further discussion. These were black cutworm, Agrotis ipsilon (Hufnagel); celery looper Anagropa falcifera (Kirby); forage looper and clover looper, Caenurgina
Table 9. Moths observed feeding in Iowa from 1986-1989. The first number under each plant is the number of males collected. The second is the number of females.

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spp. (see Willson and Bertin 1979); pale tussock moth, *Halysidota tessellaris* (Smith); European corn borer, *Ostrinia nubilalis* (Hübner); plantain looper, *Autographa precationis* (Gn.); celery leaf tier, *Udea rubigalis* (Gn.); yellowstriped armyworm, *Spodoptera ornithogalli* (Gn.); variegated cutworm, *Peridroma saucia* (Hübner); armyworm, *Pseudaletia unipuncta* (Haworth); cabbage looper, *Trichoplusia ni* (Hübner); corn earworm, *Heliothis zea* (Boddie); dingy cutworm, *Feltia ducens* (Walker); *Trache delicata* (Grt); clover cutworm, *Discestra trifolii* (Hufnagel); bristly cutworm *Lacinipolia renigera* (Steph.); *Catocala minuta* (Edw.); *Xestia tenuicula* (Morr.); and *Nomophila nearctica* (Hübner). All but four (European corn borer, celery leaf tier, *Nomophila nearctica* and pale tussock moth) were noctuids. Three of these species (pale tussock moth, clover cutworm, *Catocala minuta*) were pyralids and the last an arctiid. The sex ratios of these feeding insects were strongly biased toward males (Table 10). The feeding activity of three species, however, was largely dominated by females.

The seasonal trend for black cutworm includes a large peak of activity early in the season, with a second peak at 7 wk (Figure 14). Hourly black cutworm feeding on all plants showed a maximum activity peak at approximately 2.5 hr after dusk (Figure 15). Males appeared in large numbers early in the evening followed by a rapid decline. Numbers of females did not decline as rapidly. All reproductive classes of females were found. Eight class I females were collected, while 8, 8 and 7, respectively, were collected of class II through IV.
Table 10. Overall four-year sex ratios of selected moths observed feeding

<table>
<thead>
<tr>
<th>Common Name</th>
<th>Insect</th>
<th>Sex Ratio (M:F)</th>
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</thead>
<tbody>
<tr>
<td>Black cutworm</td>
<td><em>Agrotis ipsilon</em> (Hufnagel)</td>
<td>2.4:1</td>
</tr>
<tr>
<td>Celery looper</td>
<td><em>Anagrapha falcifera</em> (Kirby)</td>
<td>1.6:1</td>
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<tr>
<td>Forage looper/clover looper</td>
<td><em>Caenurgina</em> spp.</td>
<td>1:1</td>
</tr>
<tr>
<td>Pale tussock moth</td>
<td><em>Halysidota tessellaris</em> (Smith)</td>
<td>0:11</td>
</tr>
<tr>
<td>European corn borer</td>
<td><em>Ostrinia nubilalis</em> (Hübner)</td>
<td>1.4:1</td>
</tr>
<tr>
<td>Celery leaf tier</td>
<td><em>Udea rubigalis</em> (Gn.)</td>
<td>1.8:1</td>
</tr>
<tr>
<td>Yellowstriped armyworm</td>
<td><em>Spodoptera ornithogalli</em> (Gn.)</td>
<td>1.3:1</td>
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<tr>
<td>Variegated cutworm</td>
<td><em>Peridroma saucia</em> (Hübner);</td>
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<td>Armyworm</td>
<td><em>Pseudaelia unipuncta</em> (Haworth)</td>
<td>1.2:1</td>
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<tr>
<td>Cabbage looper</td>
<td><em>Trichoplusia ni</em> (Hübner)</td>
<td>1.2:1</td>
</tr>
<tr>
<td>Corn earworm</td>
<td><em>Heliothis zea</em> (Boddie)</td>
<td>1.4:1</td>
</tr>
<tr>
<td>Dingy cutworm</td>
<td><em>Feltia ducens</em> (Walker)</td>
<td>2.5:1</td>
</tr>
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<td>Clover cutworm</td>
<td><em>Discestra trifolii</em> (Hufnagel)</td>
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<tr>
<td>Bristly cutworm</td>
<td><em>Lacinipolia renigera</em> (Steph.)</td>
<td>3.3:1</td>
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<tr>
<td>Plantain looper</td>
<td><em>Autographa precationis</em> (Gn.)</td>
<td>1.8:1</td>
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<tr>
<td></td>
<td><em>Trache delicata</em> (Grt)</td>
<td>1.9:1</td>
</tr>
<tr>
<td></td>
<td><em>Catocala minuta</em> (Edw.)</td>
<td>1:6</td>
</tr>
<tr>
<td></td>
<td><em>Xestia tenuicula</em> (Morr.)</td>
<td>2.3:1</td>
</tr>
<tr>
<td></td>
<td><em>Nomophila nearctica</em> (Hübner)</td>
<td>4.5:1</td>
</tr>
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</table>
Figure 14. Seasonal trend of black cutworm feeding activity. Observations are combined over a four year period. Weeks were seven day intervals with May 11 as the beginning week.
Figure 15. Hourly observations of black cutworm feeding activity on all plants combined. Observations were made in central Iowa.
No. of Moths

Time (min)

- Males
- Females
The celery looper seasonal trend indicated a sharp peak at weeks 10 through 13 (Figure 16). A smaller peak was observed in week 15. Hourly records combined over plants showed that these loopers appeared early in the evening with the males showing a strong peak at 45 min after dusk followed by a rapid decline (Figure 17). Females did not show a strong peak, but were collected over a wider range of times. Female reproductive classes were more representative of the older female. Eight, 21, 15 and 58 females were found from Class I through IV, respectively. In general, celery loopers were more common than black cutworms and fed earlier in the evening.

Enough celery loopers were collected from individual plants to examine plant preference. The activity on common milkweed was similar to the combined hourly records, except the females showed a stronger peak of feeding activity (Figure 18). Activity on whorled milkweed was strongest for males at dusk. Females peaked 30 min after dusk, then the numbers declined sharply (Figure 19). Feeding on alfalfa was most common 15 min after dusk, with several small peaks thereafter (Figure 20). Females were infrequently found on alfalfa.

The two species of *Caenurgina* showed several peaks during the summer (Figure 21). These moths were not present during the early season but appeared regularly throughout the season after week five. The *Caenurgina* complex of moths showed a trend similar to that of celery looper for hourly feeding behavior (Figure 22). Females were collected later than the males. However, the female: male ratio was higher than in the celery looper. As with the celery looper, *Caenurgina* reproductive development
Figure 16. Seasonal trend of celery looper feeding activity
No. of moths

Time (week)

Observations
Figure 17. Hourly observation of celery looper feeding on all plants combined
Figure 18. Hourly observations of feeding activity of celery looper on common milkweed
No. of Moths

Time (min)

- Males
- Females
Figure 19. Hourly observations of feeding activity of celery looper on whorled milkweed
No. of Moths

Time (min)

Males  Females
Figure 20. Celery looper feeding on alfalfa
No. of Moths

Time (min)

- Males
- Females
Figure 21. Seasonal trend of *Caenurgina* spp. observed feeding on common Iowa plants
Number of moths vs. time (week)
Figure 22. Hourly feeding behavior of Caenurgina spp. collected from all plants
No. of Moths

---

Time (min)

- Males
- Females

- 0 30 60 90 120 150 180 210
- 30 25 20 15 10 5 0

---

2.4.8
was more representative of older females. Class III and Class IV (45, 47, respectively) were twice as common as Class I and Class II (24, 24, respectively).

*Caenurgina* occurred on milkweed in large enough numbers to warrant further examination. The females were predominant over males on milkweeds (Figure 23), again showing the strong peak in time of feeding as exhibited in the combined feeding records (Figure 22). Males were much less frequent on common milkweed during the early evening than was noted from the combined feeding records. The feeding peak for males on common milkweed also occurred later in the evening than was observed overall. Feeding on alfalfa (Figure 24) comprised the bulk of records for *Caenurgina*, and therefore closely resembled the combined feeding records.

An overwhelming majority of European corn borers were collected during weeks 10 through 12 (Figure 25). Hourly feeding observations of European corn borer over all plants showed activity early in the evening (Figure 26). Males were extremely active at dusk and then numbers declined. There did seem to be an interaction between male and female activity. At the female feeding peak of 1 hr, males were not collected. Thereafter, whenever females were observed, fewer males were collected. Virgin and reproductive females were not commonly collected (0 of class I and III, 2 class II), however, 19 class IV females were found.

Collections of the variegated cutworm were largely confined to early season. A small secondary peak was observed during week 8 (Figure 27). Variegated cutworms primarily were observed during the first 2.75 hr of
Figure 23. *Caenurgina* spp. observed on common milkweed
Figure 24. *Caenurgina* spp. observed on alfalfa
No. of Moths

Time (min)

---

No. of Moths

Time (min)

Males

Females
Figure 25. Seasonal trend of European corn borer feeding activity on common Iowa plants
No. of moths

Observations

Time (week)
Figure 26. Hourly feeding behavior of European corn borer
No. of Moths

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<td>8</td>
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<tr>
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<td>8</td>
<td>10</td>
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Figure 27. Seasonal trend of variegated cutworm feeding activity
200

No. of moths

150

100

50

0

1 3 5 7 9 11 13 15 17

Time (week)

Observations
the evening (Figure 28). The males were present in much larger numbers than females during this period. The majority of variegated cutworms were obtained from lilac, which blooms in the spring (Figure 29). Feeding on alfalfa was much more erratic than on lilac and occurred later in the evening (Figure 30). Peak feeding of males coincided on the two plants. However, peak feeding of females differed considerably, depending on the host, with females on alfalfa feeding predominately at 2.25 hr after dusk. Reproductive females were commonly collected. Twelve class I, 9 class II and 23 class III females were found, compared to 11 class IV females.

During the early weeks of the study armyworm moths were collected mainly from lilac, a spring blooming plant. During week seven, the moths had shifted to grasses and alfalfa (Figure 31). Hourly feeding of armyworm moths showed a trend similar to that of the variegated cutworm (Figure 32) except that they were observed later in the evening than the variegated cutworms. Peak feeding activity was observed in both species at approximately 1.5 hr after dusk. Females were collected more frequently than males from grasses (Figure 33) and alfalfa (Figure 34). Feeding activity on the two plant species differed, however, with alfalfa being more attractive, especially to females, later in the evening. In contrast, feeding on lilac showed a gradual upward trend during the evening followed by a definite decline (Figure 35). The sex ratio was more evenly distributed on the lilac as well. The activity trend of armyworm on lilac was the antithesis of the variegated cutworm, with the former feeding in the early evening followed by a gradual decline in
Figure 28. Hourly observations of variegated cutworm feeding behavior
Figure 29. Hourly observations of variegated cutworm feeding behavior on lilac
No. of Moths

Time (min)

Males  Females
Figure 30. Hourly observations of variegated cutworm feeding on alfalfa
No. of Moths

Time (min)

--- Males  + Females

0 30 60 90 120 150 180 210 240
Figure 31. Seasonal trend of armyworm feeding behavior
No. of moths

Observations

Time (week)
Figure 32. Hourly observations of armyworm feeding activity
No. of Moths

Time (min)

- Males
- Females
Figure 33. Hourly observations of armyworm feeding activity on grass
Figure 34. Hourly observations of armyworm feeding activity on alfalfa
No. of Moths

Time (min)

0 75 150 225 300 375

0 2 4 6 8 10 12

No. of Moths

--- Males --- Females
Figure 35. Hourly observations of armyworm feeding activity on lilac
No. of Moths

Time (min)

---

- - Males
- - Females

Number of moths varies over time with peaks at different intervals.
numbers later. The females collected were predominately class II and III (65 and 68, respectively), while virgin and class IV represented 18 and 29, respectively, of the total catch.

Corn earworm moths were collected almost exclusively late in the season, primarily during week 15 (Figure 36), and were collected in the largest numbers at dusk (Figure 37) with a gradual decline thereafter. Both sexes showed a similar trend. Because the large majority of moths were collected from alfalfa, it mirrored the combined hourly trend. Female reproductive classes were similar to armyworm with the majority Class II and III (24, 24, respectively). Virgin and class IV females were not as common (14, 5, respectively).

Dingy cutworm moths were collected exclusively during the final weeks of observation (Figure 38). The majority of dingy cutworms, were observed feeding within the first hour after dusk (Figure 39). Females did not show a strong peak, but were observed in relatively constant numbers. Most dingy cutworms were collected from goldenrod (Figure 40); the feeding behavior on this plant was very similar to the combined observations from all plants (Figure 39). Thereafter, feeding observations decreased gradually until 2.5 hr after dusk. Female reproductive development was similar to the armyworm and corn earworm (7, 44, 33, 5 for classes I-IV, respectively).

The clover cutworm was collected only during discrete periods of the summer (Figure 41). A large increase of the population was observed during week 17, more than twice the number collected in the preceding
Figure 36. Seasonal trend of corn earworm feeding activity
No. of moths

Observations

Time (week)

0 10 20 30 40 50 60 70 80 90 100 110 120

1 3 5 7 9 11 13 15 17
Figure 37. Hourly observations of corn earworm feeding behavior
No. of Moths

Time (min)

- Males
- Females

[Graph showing the number of moths captured over time, with a peak around the 30-minute mark for males and a later peak for females.]
Figure 38. Seasonal trend of dingy cutworm feeding activity
No. of moths

- Observations

Time (week)
Figure 39. Hourly observations of dingy cutworm feeding activity
Figure 40. Hourly observations of dingy cutworm on goldenrod
Figure 41. Seasonal trend of clover cutworm feeding activity
No. of moths

Observations

Time (week)
weeks. The clover cutworm was collected erratically during the evening hours (Figure 42). Females appeared earlier in the evening and fed in greater numbers than the males. Reproductive development of females was again found to center on reproductively active females (5, 10, 12, 3 for classes I-IV, respectively).

Like the dingy cutworm, bristly cutworms were collected only during the final week of study (Figure 43). Bristly cutworms were found within the first 2.5 hr after dusk (Figure 44). Females declined sharply after 1.5 hr and were not noticed thereafter. Numbers of males declined at 1.75 hr but these numbers returned after 2.15 hr. Class I and Class II (3, 5, respectively) females were the only females collected.

Plantain loopers were observed in small numbers throughout the season. However, a peak occurred in week 14 (Figure 45). Both sexes of plantain looper showed greatest feeding activity 30 min after dusk (Figure 46). Several females were observed feeding at 1.50 hr after dusk as well. The reproductive stages of the female were equally represented (2, 2, 2, 1 for Class I-IV, respectively). *Catocala minuta* were collected primarily during the first weeks of the study (Figure 47). Hourly observations showed that feeding lasted until 2.75 hr after dusk with no difference in peak feeding time among sexes (Figure 48). Post-reproductive females were the most commonly collected *Catocala minuta* (7 females). Classes I-III were not commonly found (0, 2, 3, respectively). The seasonal trend of cabbage looper showed increases in the population as the season progressed (Figure 49). As with *C. minuta*, the sexes were synchronized, with a peak in feeding activity occurring 45 min after dusk.
Figure 42. Hourly observations of clover cutworm feeding activity
No. of Moths

Time (min)

- Males
- Females
Figure 43. Seasonal trend of bristly cutworm feeding activity
No. of moths

- Observations

Time (week)
Figure 44. Hourly observations of bristly cutworm feeding behavior
No. of Moths

Time (min)

No. of Moths

Time (min)

- Males
- Females
Figure 45. Seasonal trend of plantain looper feeding activity
No. of moths

Observations

Time (week)

0  5  10  15  20  25  30  35  40
Figure 46. Hourly observations of plantain looper feeding activity
No. of Moths

Time (min)

0 30 60 90 120 150

0 1 2 3 4 5 6

--- Males --- Females
Figure 47. Seasonal trend of *Catocala minuta* feeding activity
No. of moths

Time (week)

Observations

35
30
25
20
15
10
5
0

1  3  5  7  9 11 13 15 17
Figure 48. Hourly observations of *Catocala minuta* feeding activity
No. of Moths

Time (min)

- Males
- Females

0 30 60 90 120 150

0 1 2 3 4 5
Figure 49. Seasonal trend of cabbage looper feeding activity
No. of moths

- Observations

Time (week)
Young reproductive class II females were most commonly collected (10 females), with all other classes evenly represented (5, 4, 5 for class I, III, IV, respectively).

The pale tiger moth was collected primarily during weeks 10 through 12 (Figure 51). The hourly observations showed the males fed early, followed by a gradual decrease and a second peak after 1.15 hr. Female feeding activity peaked during the time when males were most scarce (Figure 52). Post-reproductive females were most commonly collected (5 females), followed by class III (3 females), class II (1 females) and class I (0 female).

Feeding on Specific Plants

The common milkweed was very attractive to a wide range of night-feeding insects. Moths alighted on the umbel, generally near the bottom florets. A moth typically extended its proboscis and inserted it into the individual flowers, slowly working the flower head. Moths engaged in feeding were not readily disturbed and could be collected easily. The flowers of the milkweed were highly fragrant and the odor could be discerned from a distance. Moths often flew upwind to the flowers. During the killing process (described in Material and Methods), the abdomens would frequently burst, exuding nectar. Feeding activity began at dusk, peaked within the hour and fell sharply thereafter ceasing by 5 hr after dark (Figure 53). With males, a small secondary feeding peak was observed shortly after the first. Male and female moths were found to feed in equal numbers (M:F 1:1.03).
Figure 50. Hourly observations of cabbage looper feeding activity
No. of Moths

0 30 60 90 120

Time (min)

No. of Moths

0 1 2 3 4 5 6 7 8

Males
Females
Figure 51. Seasonal trend of pale tiger moth feeding activity
No. of moths:

- Observations

Time (week):

0 1 3 5 7 9 11 13 15 17

- Observations
Figure 52. Hourly observation of pale tiger moth feeding activity
No. of Moths

- Males
- Females

Time (min)

0 15 30 45 60 75 90 105 120

10 8 6 4 2 0
Whorled milkweed was not visited by moths as frequently as common milkweed, and the feeding behavior of these moths also differed (Figure 54). Male activity began at dusk and numbers fell sharply thereafter. Female activity occurred later. Moth visitations were not observed as late in the evening as on the common milkweed. Most feeding had ceased by 2.75 hr after dusk.

Alfalfa was very attractive to adult moths (Figure 55), but their feeding behavior was different than that on the milkweeds. Flowers were sparser and moths took to flight more readily than those on milkweeds. Males were more commonly encountered than females (M:F 1.4:1). Observations of both sexes indicated that feeding began at dusk and decreased slowly thereafter. Feeding was observed over a 6.75 hr period, although most activity had ceased after 4 hr.

Goldenrod bloomed later during the collection season and was the only plant commonly found in bloom at this time. Goldenrod, therefore, was visited by a large number of moths (Figure 56). Although flowers occurred in large heads, the feeding behavior was similar to that observed on alfalfa. As the evening progressed and temperatures dropped, however, moths were less likely to take flight. Male activity peaked earlier in the evening than female activity. All feeding ceased by 2.5 hr after dusk. Because of the lateness in the season, temperatures were generally very cool during this part of the study.

Lilac was very attractive to early season moths. Feeding behavior was similar to that on milkweeds. The flowers were very fragrant, and the flower heads commonly had more than one insect feeding
Figure 53. Attractiveness of common milkweed to night feeding moths. Observations presented in 15 min intervals.
No. of Moths

![Graph showing the number of moths over time for males and females.](image)

- **Males**
- **Females**

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Figure 54. Attractiveness of whorled milkweed to night feeding moths. Observations presented in 15 min intervals
No. of Moths

Time (min)

-- Males  +  Females
Figure 55. Moth feeding activity on alfalfa
simultaneously. As with the milkweed, abdomens of collected insects would often burst, exuding nectar. Because the lilacs were in bloom early in the season, temperatures were cool and the moths less likely to take flight. Feeding activity began gradually after dusk, peaked, then slowly declined (Figure 57). Activity ceased by 3 hr after dusk.

Minor plant hosts included the grasses. Moths were observed to feed at the seed head. Feeding behavior was similar to that on alfalfa. Wild carrot, red clover, and sweet clover also attracted several moth species (Table 9). Again, feeding behavior of moths was similar to alfalfa.

Pollen Carried by the Insects

It is evident from examining pollen loads (separated by plant species) that moths feeding on nectar also carry lilac pollen and could possibly act as pollinators (Figure 58). All moths collected from lilac carried pollen on the proboscis. In contrast, moths feeding on whorled milkweed, red clover, wild carrot, Indian hemp and honeysuckle infrequently carried pollen. Approximately one-half of the insects feeding on goldenrod carried pollen. This was also true for insects feeding on campion and clump bush. One-third of the moths that visited alfalfa and common milkweed carried pollen.

Only moths visiting milkweed carried significant numbers of pollinia (Figure 59). Just 20% of the moths collected from milkweed, however, carried the pollinia. Nine percent, 5.1% and 3.9% of the moths collected from whorled milkweed, grass and alfalfa, respectively carried pollinia or pollen. Overall, pollinia were infrequent on collected moths.
Figure 56. Moth feeding activity on goldenrod
No. of Moths

Time (min)

- Males
- Females
Figure 57. Moth feeding activity on lilac
No. of Moths

Time (min)

- Males
- Females
Figure 58. Percentage of moths carrying pollen from thirteen species of common Iowa plants
The percentages of moths bearing pollen are presented for five species in Figure 60. Sixty percent of the black cutworm moths carried pollen and 29.0% of the captured celery loopers and 28.8% of *Caenurgina* spp. bore pollen. Only 4.6% of the European corn borers were found with pollen. As with the black cutworm, a majority of the variegated cutworms examined (81.0%) bore pollen loads. Percentages for six more moth species are shown in Figure 61. Nearly 53% of the captured armyworm were carriers of pollen, but just 29.4% and 29.3% of the cabbage loopers and corn earworm moths, respectively, bore pollen. Almost one-half of dingy cutworm moths (45.6%) had pollen. Similar to the black cutworm, 63.8% of the clover cutworm moths carried pollen, while only 36.4% of the bristly cutworms carried pollen. With one exception, less than 10% of the moths in each species discussed above, carried pollinia. Only the clover cutworm (10.4%) commonly carried pollinia.
Figure 59. Percentage of moths carrying milkweed pollinia from four species of common Iowa plants
No. of Moths

- Common milkweed
- Whorled milkweed
- Grasses
- Wild Carrot
- Alfalfa

- Moths w/o pollinia
- Moths with pollinia

Plant
Figure 60. Percentage five moth species observed feeding that were carrying pollen
No. of Moths

Black cutworm
Celery looper
Caenurgina
European corn borer
Variegated cutworm

Insect

Moths w/o pollen
Moths with pollen
Figure 61. Percentage of six moths species observed feeding that were carrying pollen
These results expand the feeding records of 36 species of moths. Similar to the results reported by Norris (1936), noctuids were more common than the geometrids (28 and 2 species, respectively) at feeding sites.

One of the most significant findings was the observations of 65 European corn borers imbibing nectar. This is the first account of feral moths feeding on substances other than water. The European corn borer has not been recorded feeding on nectar. Moths have been observed to feed solely upon water, primarily in the form of dew (Drake 1926, Spencer and Crawford 1923, DeRozari et al. 1977). Drinking water was found to be essential for good egg production and for satisfactory hatchability of the eggs (Kira et al. 1969). However, the borer has a well-developed proboscis capable of nectar feeding (Miller 1988) and other Pyralids are known to feed at nectaries (Campbell and Pike 1985). Although not completely indicative of nectar feeding, two European corn borers, among many other pyralids, were collected at a trap baited with the bladder flower, Araujia sericofera Brot (Cantelo and Jacobson 1979). The bladder flower contains phenylacetaldehyde and attracts many nocturnal insects including corn earworm and armyworm. Honey in water imbibed by the female might increase production of eggs (Miller 1988). Four differences were found in favor of honey-water feeding: a greater proportion of unlaid eggs were mature; fewer expired females contained immature oocytes; late eggs were heavier; and more females maintained or increased
egg weight during the oviposition period. Interestingly, female life span was shorter for the honey-water feeders.

Wynne and Keaster (1987), concentrating mainly on trees, observed black cutworm feeding on a variety of hosts. Therefore, most of their feeding records were not duplicated in this study. Observations on common milkweed and red clover, however, were reiterated. Further, our study expanded the Wynne and Keaster (1987) study by providing information about female ovipositional development and nocturnal feeding patterns. *Melilotus* spp., *Bromus* spp., wild carrot, goldenrod, Joepye weed and lilac were new adult host plants.

The results concerning moth feeding on milkweeds compare favorably with studies conducted by others (Willson et al. 1979, Willson and Bertin 1979). Contrary to their results, however, black cutworm and variegated cutworm were not found to be the primary night pollinators. Celery loopers and *Caenurgina* spp. were the most common on milkweeds in Iowa.

Collection of feeding females showed a large range of diversity in reproductive development. European corn borer females were almost exclusively post-reproductive. Evidently, nectar uptake is not necessary for egg-laying or more reproductive females would be represented. Although Miller (1988) found a food source can produce some advantage for egg production, feral reproductive females are not strongly attracted to nectar sources. Both *Catocala minuta* and pale tiger moth females were also predominately post-reproductive. The rest of the moth species were found to be evenly distributed or biased toward reproductive females. The nectar source provides energy for daily functions and for egg-laying.
Greater than 50% of the moths of some species were found to carry pollen. These pollen loads suggest that some species are indeed important transporters of pollen. Some plant species, i.e., lilac, were more receptive for pollen dissemination. All moths collected from lilac were found to carry pollen. Therefore, as discussed by Bertin and Willson (1980), these nocturnal nectar visitors can be effective pollinators.
PART IV. TRACING BLACK CUTWORM, AGROTIS IPSILON (HUFNAGEL)
AND ARMYWORM, PSEUDALETIA UNIPUNCTA (HAWORTH)
(LEPIDOPTERA: NOCTUIDAE), MIGRATION USING POLLEN ANALYSIS
INTRODUCTION

Circumstantial evidence of black cutworm, *Agrotis ipsilon* (Hufnagel), migration has accumulated since the discovery of mass spring flights along the Nile Valley and the coast of the Red Sea (Williams 1924, 1926). Spring captures in Iowa of black cutworm males in traps baited with sex pheromone were associated with brisk southerly winds (Kaster and Showers 1982). A systematic transport rating system was developed to identify climatic conditions favorable for black cutworm moth introduction to Iowa from the south, and to differentiate them from those required for local flights (Domino et al. 1983). Correspondence of males captured in sex pheromone-baited traps with transport ratings (Domino et al. 1983) indicated that in early spring, Iowa and northern Missouri moth populations are composed of introduced individuals.

Black cutworms were marked with fluorescein after capture at feeding stations in southern China (Jia et al. 1985). Moths recaptured at feeding stations various distances from the release sites were assayed for the dye with thin-layer chromatography. The authors do not indicate the numbers marked and released but, in the three years of study, they recaptured 8 moths at distances as far as 1818 km north of the release site.

The armyworm, *Pseudaletia unipuncta* (Haworth) was first considered migratory during the massive 1914 outbreak in North America (see Breeland 1958). Additional work with ovarian development (McNeil 1987) and overwintering potential (Fields and McNeil 1984), has provided
circumstantial evidence for long-distance movement. Empirical evidence, such as the mark-release-recapture technique used for black cutworm, has been deficient.

Pollen analysis can be useful to study migration (Hendrix et al. 1987) because many plants depend on insects for pollination. Such plants have evolved pollen that adheres readily to the exteriors of insects. Moths dusted with pollen, therefore, are naturally marked. Identification of these pollens to plant family can often locate the geographic origin of the plants, and hence the origin of the carrier moth. Pollen analysis has been used for studies of immigrants in Finland (Mikkola 1971). Pollens were removed from dried museum specimens and examined. Six A. ipsilon were examined and a single pollen grain of Corylus was found. In total, 13 species were searched for pollen but the distributions of the identified plants overlapped the origin and deposition sites of the migrants.

Pollen has also been used as an indicator of the long-distance movement of H. zea into Arkansas (Hendrix et al. 1987). Two Mimosoideae legumes, Pithecellobium and Calliandra, were discovered on spring moths captured in Arkansas. The nearest populations of these genera are located in southern Texas. In total, 18 moths were collected by Hendrix et al. (1987) with these exotic pollens adhering to the eyes or proboscis indicating migration of 1000 km or more.

The objective of this study was to confirm black cutworm and armyworm migration over long distances by tracing the origin of naturally marked
moths through identification of pollen. The results also shed light on the specific regions of origin of Iowa spring immigrants.
MATERIALS AND METHODS

From 1985 to 1988, black cutworm were collected from wing style sex pheromone traps in Ankeny (Central), Iowa; Maryville (North), Missouri (1985 only) and a trap line running through Topeka, Kansas to St. Louis (Central), Missouri. Armyworm moths were collected only from Central Iowa pheromone traps. Traps were baited with commercially prepared sex pheromone for each species. Both male and female black cutworm and armyworm moths were collected from a blacklight trap during 1985-1988. Moths were collected from first capture in the spring until 31 May.

Moths were placed individually in 21 ml plastic cups and frozen until examination. Moths collected during 1986 were unusable because of a malfunction in the freezer. Moths were examined at 100x magnification to locate pollen and to allow some identification of these pollens. To prevent contamination, 9-cm paper toweling was placed on the microscope stage and changed after examination of each collection sample. Likewise, all forceps and teasing needles were cleaned after examination of each collection sample. Selected pollen-bearing moths were studied under a phase-contrast microscope to further aid identification.
RESULTS AND DISCUSSION

Over the three years of study, 2490, 146, 2283 and 174 moths of male black cutworm, female black cutworm, male armyworm and female armyworm, respectively, were collected in Central Iowa and examined for pollen. During the 1985 collection season, 442 black cutworm moths from Central Missouri and 280 black cutworms from North Missouri were examined. The percentage of moths carrying pollen varied from 30% to 65% for female armyworm and male black cutworm, respectively (Table 11). Most commonly, pollen was found on the proboscis, but occasionally on the eye and other parts of the body (Table 11). When pollen was found on the proboscis, typically many grains were present. Only rarely were one or two grains found. This suggests active contact through feeding, rather than casual contact through wind blown contamination, for example.

During the entire experiment 5755 moths were examined and a total of 14 moths (0.24%) were found to carry *Pithecellobium* or *Calliandra* polyads or pollen masses (Table 12). *Pithecellobium* and *Calliandra* are legumes of the neotropics. Their nearest location to Iowa and Missouri is south Texas. During 1985, some moths from all locations were captured that carried *Pithecellobium*. In general, the more southerly the latitude with moth capture the earlier the capture (Figure 62). It is important to note that a female black cutworm was also collected with *Pithecellobium*, providing positive evidence for immigration of the female. Thus the results of mark-release-recapture studies, such as those by Showers et al. (1989a), that utilize only the male can more confidently be
Table 11. Percentage distribution of pollen on black cutworm and armyworm moths collected during 1985-1988 in central Iowa, north Missouri and central Missouri^1

<table>
<thead>
<tr>
<th>Location</th>
<th>Central IA</th>
<th></th>
<th>North MO</th>
<th></th>
<th>Central MO</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>black cutworm</td>
<td>armyworm</td>
<td>black cutworm</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>male</td>
<td>female</td>
<td>male</td>
<td>female</td>
<td>male</td>
</tr>
<tr>
<td>with pollen</td>
<td>65.1%</td>
<td>38.4%</td>
<td>46.7%</td>
<td>30.0%</td>
<td>35.0%</td>
</tr>
<tr>
<td>located on the</td>
<td>92.0%</td>
<td>81.8%</td>
<td>94.0%</td>
<td>78.8%</td>
<td>54.8%</td>
</tr>
<tr>
<td>proboscis</td>
<td>14.6%</td>
<td>30.3%</td>
<td>27.5%</td>
<td>30.8%</td>
<td>37.4%</td>
</tr>
<tr>
<td>located on the</td>
<td>13.7%</td>
<td>45.5%</td>
<td>7.0%</td>
<td>3.8%</td>
<td>26.5%</td>
</tr>
<tr>
<td>eye</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>located on</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>elsewhere^3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

^1Percentages would exceed 100% because pollen could be found in more than one location.
^2Moths were collected from north Missouri only during 1985.
^3If pollen was not on the proboscis and eye, it was commonly on the antennae.
Table 12. Moths collected in central Iowa, north Missouri and central Missouri that have *Pithecellobium* and *Calliandra* exotic pollen

<table>
<thead>
<tr>
<th>Date</th>
<th>Location</th>
<th>Pollen</th>
<th>Insect</th>
</tr>
</thead>
<tbody>
<tr>
<td>1985</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>25 March</td>
<td>Central MO</td>
<td><em>Pithecellobium</em></td>
<td>male black cutworm</td>
</tr>
<tr>
<td>28 March</td>
<td>North MO</td>
<td><em>Pithecellobium</em></td>
<td>male black cutworm</td>
</tr>
<tr>
<td>1 April</td>
<td>Central MO</td>
<td><em>Pithecellobium</em></td>
<td>male black cutworm</td>
</tr>
<tr>
<td>10 April</td>
<td>North MO</td>
<td><em>Pithecellobium</em></td>
<td>male black cutworm</td>
</tr>
<tr>
<td>20 April</td>
<td>North MO</td>
<td><em>Pithecellobium</em></td>
<td>male black cutworm</td>
</tr>
<tr>
<td>21 April</td>
<td>Central IA</td>
<td><em>Pithecellobium</em></td>
<td>male armyworm</td>
</tr>
<tr>
<td>22 April</td>
<td>Central IA</td>
<td><em>Pithecellobium</em></td>
<td>female black cutworm</td>
</tr>
<tr>
<td>25 April</td>
<td>North MO</td>
<td><em>Pithecellobium</em></td>
<td>male black cutworm</td>
</tr>
<tr>
<td>28 April</td>
<td>Central IA</td>
<td><em>Pithecellobium</em></td>
<td>male black cutworm</td>
</tr>
<tr>
<td>10 May</td>
<td>North MO</td>
<td><em>Pithecellobium</em></td>
<td>male black cutworm</td>
</tr>
<tr>
<td>25 May</td>
<td>Central IA</td>
<td><em>Pithecellobium</em></td>
<td>male black cutworm</td>
</tr>
<tr>
<td>1987</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7 May</td>
<td>Central IA</td>
<td><em>Pithecellobium</em></td>
<td>male black cutworm</td>
</tr>
<tr>
<td>16 May</td>
<td>Central IA</td>
<td><em>Calliandra</em></td>
<td>male black cutworm</td>
</tr>
<tr>
<td>25 May</td>
<td>Central IA</td>
<td><em>Calliandra</em></td>
<td>male black cutworm</td>
</tr>
</tbody>
</table>
Figure 62. Moths collected during 1985 from central Iowa, north Missouri and central Missouri with *Pithecellobium* polyads attached to the eye.
generalized to the entire population. Two moths collected in 1987 were found to have *Calliandra* polyads attached to the eye and a single moth carried *Pithecellobium*. No moths from 1988 were found to have these polyads.

The pollen of *Pithecellobium* is a polyad of 16 cells and is approximately 100μm in diameter. The polyads attach to the eye via a sticky exine. There are no specialized structures for air transport. *Pithecellobium* blooms in April at Brownsville, Texas (Isley 1972) so the early captured moths must have originated south of Texas. *Pithecellobium* dulce has been collected by the author in Tampico, Mexico in mid-March when the Brownsville species were not yet blooming. *Calliandra* is a low perennial herb or shrub. Again, all species are in bloom during immigration periods. The pollen is a bilateral, flattened octad (Sorsa 1969) approximately the same size as *Pithecellobium*. Assuming the nearest source of all moths carrying these exotic pollens was south Texas, the moths traveled at least 1300 km to Central Missouri, 1450 km to North Missouri, and 1600 km to Central Iowa. Moths collected during March (Table 12) would have originated a minimum of 600 km further south.

The pollination biology of these legumes is not well known. It is of importance, however, that all of the polyads were attached to the same general area on the compound eye, offering clues about the pollination mechanism. With *C. haemacephala* Hassk., a related *Calliandra*, the anthers are attached in a median position at right angles to the axis of the filaments. Thus, the face of the anther is directed away from the center of the inflorescence. Between the apices of the foot grains an
extremely viscous substance is formed. At anthesis, the polyads are held with their apices directed outward. Each apex is covered by a glistening drop of adhesive material to attach it firmly to the pollinator. *Calliandra* flowers were examined for the presence of moth scales and the flowers were thought to be moth pollinated (Cruden et al. 1976). Unfortunately, no attempt was made to find the pollinators. Also, large volumes of nectar were found to be produced by the flowers of *C. anomala* (Cruden et al. 1976).

Like *Calliandra, Pithecellobium* is also pollinated by night flying insects (Janzen 1982). Field observers found the nectaries very active in the evening and early morning (Elias 1972). Further, the activity of the nectaries coincides with pollen maturation. Nectar activity ceased after pollination or fertilization. In the American tropics, flowers of *P. saman* begin to open daily at 1500 hr and most are open fully by 1700 hr. Nectar flow begins between 1600-1700 hr. Mean nectar production per inflorescence averages 14.5 microliters (Jones 1983).

The aforementioned studies have shown that night-flying moths are attracted to the flowers of *Calliandra* and *Pithecellobium*. Both black cutworm and armyworm feed within the first 175 min after dusk (see Part III), during the same time the legume flowers are receptive. The moths collected in this study were collected in Iowa and Missouri when the plants were in bloom within their endemic range. The presence of pollen of these two legume species on moths captured outside the plant’s range, therefore, offers empirical evidence for long-distance migration of black cutworm and armyworm.
SUMMARY

Daily timing of adult eclosion for black cutworm and armyworm was examined. Armyworm emergence cycles were affected by cold storage. Pupal emergence was inhibited, regardless of colony age. Conversely, black cutworm colonies show a laboratory rearing effect, with the colony residing in the laboratory the longest being selected for earlier emergence. The length of the emergence cycle was the same for both black cutworm and armyworm. Differences between sexes were not observed for the emergence cycle of either species. Although both species had peak emergence at 2200 hr, the armyworm began emergence more readily after onset of darkness. The bulk of black cutworm eclosion was skewed to the 2200 and 0200 hr periods. Effects of cold storage on black cutworm colonies was evident. The black cutworm colony reared under laboratory conditions the longest was most strongly affected, with a weakening of the emergence peak. Standard rearing temperature spreads the emergence times of two-year-old laboratory colonies of armyworm from the peak time period. Cold storage negates the sharp emergence peak of an armyworm colony in the laboratory less than one year. Cold storage affected emergence of the sexes of black cutworm. Males emerged in greater proportion than females with the onset of dark. Females emerged in greater numbers later in the evening with a second peak at 0600 hr. Cold storage, however, offers a practical method of controlling the time of emergence for these two species.
Posteclosion feeding of laboratory reared black cutworm and armyworm was also investigated. Over 70% of both species fed in the laboratory within one hour after eclosion, and nearly 87% fed within six hours. Even deformed moths, without expanded wings, take food. The results of this research show that a large majority of black cutworm and armyworm feed if food sources are available. Feeding activity seemingly is critical for migration.

Nocturnal feeding on common plants of Iowa was observed in the field. Moths were collected feeding on: common milkweed, *Asclepias syriaca* (L.) (Asclepiadaceae); whorled milkweed, *Asclepias verticillata* (L.) (Asclepiadaceae); sweet clover, *Melilotus officinalis* (L.) and *Melilotus albus* (Desr.) (Leguminosae); red clover, *Trifolium pratense* (L.) (Leguminosae); white campion, *Lychnis alba* (Mill.) (Caryophyllaceae); brome grass (Gramineae); wild carrot, *Daucus carota* (L.) (Umbelliferae); alfalfa, *Medicago sativa* (L.) (Leguminosae); bull thistle, *Cirsium vulgare* (Savi) (Compositae); Indian hemp *Apocynum cannabinum* (L.) (Apocynaceae); tall joepy weed, *Eupatorium altissimum* (L.) (Compositae); goldenrod, *Solidago* sp. (Compositae); smartweed, *Polygonum* sp.; common lilac, *Syringa vulgaris* (L.) (Oleaceae); honeysuckle, *Lonicera morrowi* (L.) (Caprifoliaceae).

A total of 2296 moths were collected comprising 36 species and representing the families Noctuidae (28 species), Pyralidae (4 species), Arctiidae (2 species) and Geometridae (2 species). The first observation of feral European corn borer feeding on nectar was recorded.
All moths collected from lilac carried pollen on the proboscis. In contrast, moths feeding on red clover, wild carrot, Indian hemp and honeysuckle did not carry pollen at all. Moths feeding on goldenrod were evenly divided between moths carrying pollen and moths not carrying pollen. Moths feeding on campion and tall joepye weed were also evenly divided between those carrying pollen and those not carrying pollen. One third of the moths visiting alfalfa and common milkweed were carrying pollen. Only moths visiting milkweed and alfalfa were found to carry substantial numbers of milkweed pollinia.

Fingerprinting black cutworm and armyworm moth by identifying the pollen attached to each moth provided a novel technique for recognizing necessary food plants before initiation of long-range movement of these noctuids. Pollen was found primarily on the proboscis and in decreasing frequency on the eyes, legs and antennae. Fourteen moths (including a single male armyworm and female black cutworm) collected in Iowa and Missouri were marked with the exotic pollens *Pithecellobium* spp. and/or *Calliandra* spp. These plants are indigenous to southern climes and the closest site of origin to the capture points is in south Texas.

These moths have traveled from the closest plant location in Texas, 1300 km to Central Missouri, 1450 km to North Missouri, and 1600 km to Central Iowa, respectively. Moths captured in March must originate a minimum of 600 km further south than those captured in late April and May. Known exotic pollen was discovered on moths captured during May in Iowa, but these same pollens were found on moths captured earlier in
Missouri. These results provided evidence for immigration into Missouri from a more southern location within Mexico.

This research has provided information on adult behavior of several Iowa lepidopterous pests. The analysis of pollen provided conclusive evidence for immigration of black cutworm. In conjunction with previous findings (Showers et al. 1989a, Showers et al. 1989b), this portion of the research provides irrefutable evidence for immigration of this important noctuid. Eclosion and laboratory feeding studies provided further refinement for understanding important behavior of the prereproductive, and potentially migrant, moth species. Besides providing new feeding records for common moths found in Iowa, the feeding observations of feral moths might also provide information for phytoattractants for moths.
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