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THE POLLINATION ECOLOGY OF
<u>ASCLEPIAS</u> <u>INCARNATA</u> L. SUBSP. <u>INCARNATA</u>

A Thesis
Presented to the
Department of Biology
and the
Faculty of the Graduate College
University of Nebraska

In Partial Fulfillment
of the Requirements for the Degree
Master of Arts
University of Nebraska at Omaha

by
Thomas S. Brotherton
August 1984

THESIS ACCEPTANCE

Accepted for the faculty of the Graduate College, University of Nebraska, in partial fulfillment of the requirements for the degree Master of Arts, University of Nebraska at Omaha.

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THE POLLINATION ECOLOGY OF ASCLEPIAS INCARNATA L. SUBSP. INCARNATA

ABSTRACT

The pollination ecology of Asclepias incarnata L. subsp. incarnata was studied at three sites in eastern Nebraska and one in western Iowa. A. incarnata was shown to be visited by many species of insects. A few Hymenoptera and Lepidoptera served as efficient pollinators, while the other visitors were primarily nectar thieves. On disturbed sites, Megabombus pennsylvanicus (DeGeer) was the prevalent pollinator, along with Apis mellifera L., Pyrobombus griseocollis (DeGeer), and two species of Sphecinae. On undisturbed sites, A. incarnata was found in much smaller populations and was pollinated by Papilio glaucus L., Danaus plexippus (L.), Epargyreus clarus (Cramer) and other Papilio species. Several Hemipterans, Coleopterans and Homopterans were common herbivores on this plant. Nectar production appeared to peak in the morning hours and decline through the afternoon and evening, with a similar pattern of pollinator occurence. Although primarily insect pollinated, the plant apparently is capable of self-fertilization to some extent and may occasionally be apomictic or autogamous. Fruit production was affected by numerous factors, including insect predation on pollinators, insect damage to plant and immature fruit, and climatic factors.

INTRODUCTION

The swamp milkweed, Asclepias incarnata L. subsp. incarnata is a native perennial herb of central and eastern North America. It is one of 108 especially well-defined species of Asclepias indigenous to this continent. The genus Asclepias is represented by less than a dozen species in South America and by over 100 species in southern and eastern Africa. It was monographed for North America by Woodson (1954), and most of the descriptive material which follows is based on that work. Asclepiads are essentially temperate to tropical in distribution, with most of the North American species preferring rather open dryish plains, barrens or woods.

The swamp milkweed, one of only two subaquatic Asclepias species in North America, is found in open swamps, wet ditches, wet prairies, and at the edge of open water. It may become weedy, due to its ecological tolerance and apparent colonization of disturbed or damaged areas.

Asclepias incarnata has a short rootstock with numerous radiating fibrous roots. The stems are stout and erect, attaining a height of up to 1.5 meters and are repeatedly branched above. There are no rhizomes, and thus this species does not form clones as does the more common A. syriaca L. The decussate leaves are narrowly oblong to linear-lanceolate. The umbelliform inflorescences arise from the nodes and typically have many small flowers.

Within the flowers, the anthers and stigmas adhere to form a columnar gynostegium. The anthers conceal the five stigmatic surfaces, except for vertical clefts, termed alar fissures (Fig. 1). Projecting laterally are five hoods, collectively termed the corona, which act as upturned cups for the nectar. From within each hood, a horn extends up and curves inward over the top of the gynostegium. The corolla reflexes at anthesis and is distinctly red-pink in color. The pollen is produced in compact sac-like masses, termed pollinia, which are joined in pairs by translator arms to a grooved corpusculum. The corpusculum is situated at the upper end of the alar fissure, its groove aligned with the stigmatic opening (Figs. 1 and 2). The pair of pollinia, translator arms, and corpusculum are collectively termed a pollinarium (Fig. 3).

Visiting insects find the gynostegium very slick with nectar and shaped so that good footing is difficult to attain. The insect attempts repeatedly to secure a stable foraging position, often trying to grip the hood bases. The hoods' shape directs the legs between them and upward into or along the anthers and alar fissure. A hair, spine, or claw on the leg may contact the grooved corpusculum and by a wedging action, the corpusculum becomes attached to the leg. Insects may also have their mouthparts, particularly labial palps, become stuck in the corpusculum. The pollinarium is withdrawn as the insect, often struggling to free itself, leaves the flower. Corpuscula can equally well attach to the translator arms of previously withdrawn and attached pollinaria, resulting in chains of pollinaria (Fig. 4).

As the insect continues foraging, the translator arms dry,

Figure 1. *Asclepias incarnata* L. flower, lateral view. Diagram is 12X. (c = corpusculum, af = alar fissure, cd = corona hood, cn = corona horn, co = corolla)

Figure 2. *Asclepias incarnata* L. gynostegium, from above. (18X). (c = corpusculum, af = alar fissure, cd = corona hood)

Figure 1.

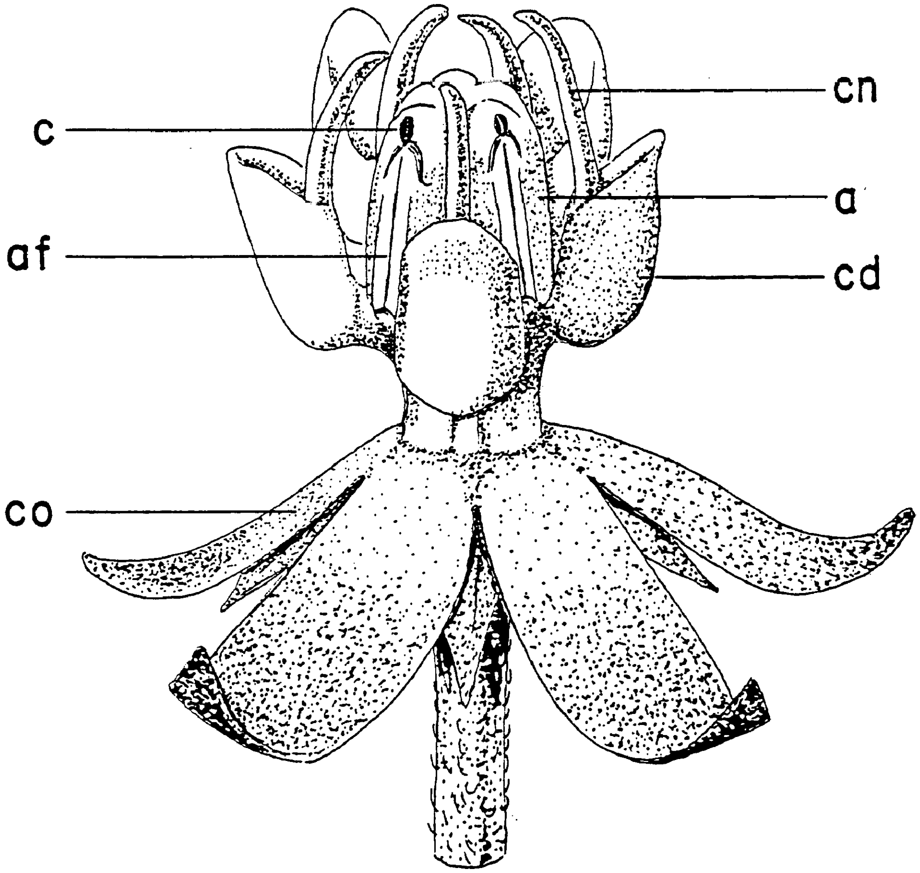


Figure 2.

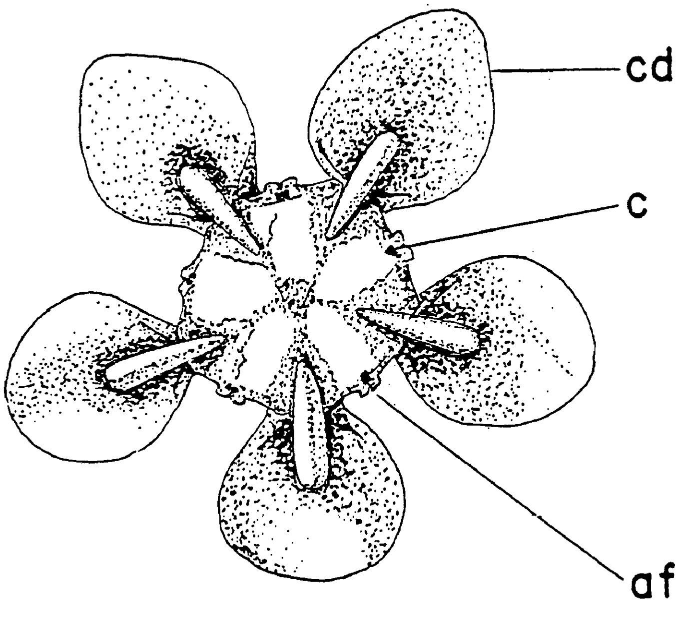
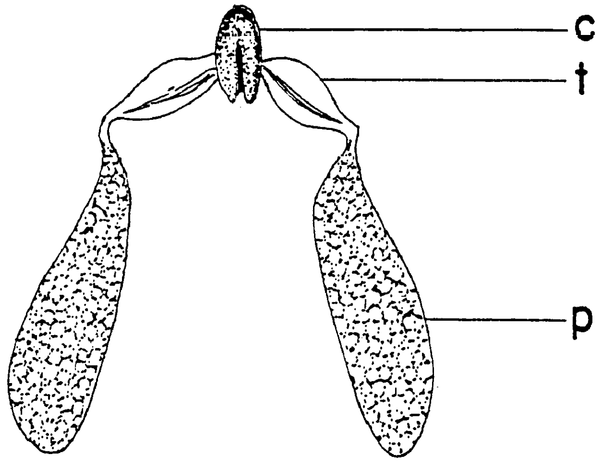


Figure 3. *Asclepias incarnata* L. pollinarium. (25X). (c = corpusculum, t = translator arm, p = pollinium)

Figure 4. *Apis mellifera* L. mesothoracic tarsus with attached *Asclepias syriaca* L. corpusculum (a) and *Asclepias incarnata* pollinaria. (25X). The pollinaria show the conditions described in the text: intact, lacking one pollinium, lacking both pollinia, and corpusculum only.

Figure 3.



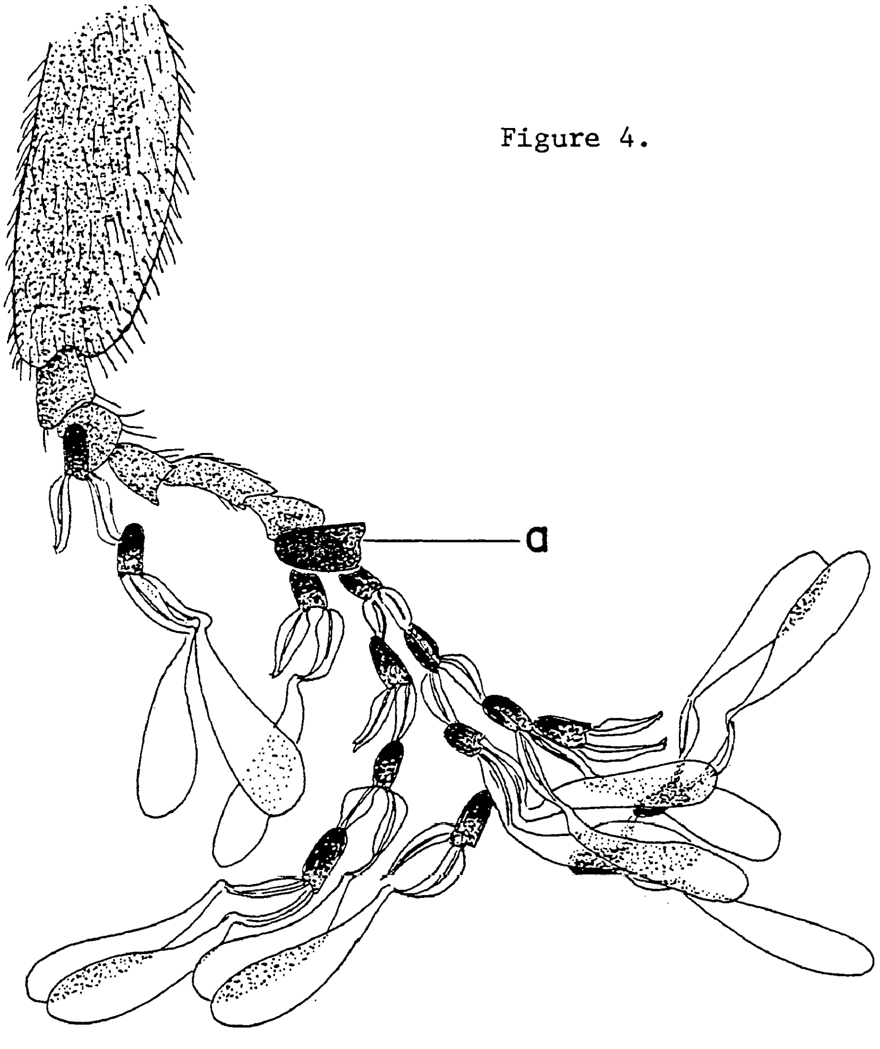


Figure 4.

reorienting the flattened pollinia to a postion at right angles to the original plane. When the leg is drawn up between the hoods of successive flowers, the pollinia may be pulled up into the alar fissure, break from the translator arm and complete pollination.

The genus *Asclepias* has received much work because of its well defined species and very low rate of hybridization, its low rate of fruit maturation versus the large number of flowers presented, and its complicated pollination mechanism. *A. incarnata* has been included in many papers, for example Macior (1965), Kephart and Heiser (1980), and Kephart (1981), which discuss its species isolation from partially sympatric *A. syriaca* and *A. verticillata*.

The intent of this study was to record the general ecology of the swamp milkweed, including its habitat preference, growth characteristics, and the flora associated with the habitat. Special attention was given to the insect visitors and their behavior. Nectar production was also considered, along with limited tests for apomixis or autogamy, self-fertility, and nocturnal versus diurnal pollinators. The plants were observed through fruiting, adding information on seed production and insect damage.

METHODS AND MATERIALS

Study Location

Four sites were utilized in this study. The primary site, designated as WD, was west of Omaha, Douglas County, Nebraska (NW¼NW¼ S22 T15N R10E). Study site two, designated L, was immediately south of WD (SW¼SW¼ S27 T15N R10E). Both of these sites had been subjected to major disturbance, either mowing or grading in the past five years. Sites three and four were in undisturbed and protected nature preserves. Number three was in Sarpy County, Nebraska in lower Fontenelle Forest Nature Center (FF), (NW¼NW¼ S19 T14N R14E), approximately 350 meters south of Child's road on the Stream Trail. Site four, in Harrison County, Iowa was in Desoto National Wildlife Refuge, (DS), (N½NE¼ S22 T18N R12E). Several plants were located along the edge of the water, due east of the Bullhead Pond parking area.

Procedures

Life History: The four sites were visited in early June to locate study populations and begin recording growth characteristics. These records were maintained through fruiting, until late October, and documented with many photographs. Collections of plants were made from WD and L to identify flora associated with *Asclepias incarnata*. Field identifications of the associated flora at FF and DS were made, but no specimens were collected.

Bagging Tests: The inflorescences of 20 plants were bagged and the plants staked, using 29 by 33 cm bags of 1 mm mesh, sewn on three sides, laced shut below and secured to 2 m stakes. The plants were loosely secured in two places along their length and at the bag with gardening twist-tie. All 20 plants were bagged within a four day period from July 14-17, when flower buds were fully formed, yet before anthesis.

Three of the bagged plants, one each at sites WD, L, and DS, were checked frequently, but not uncovered until flowering had ended and fruiting had begun. This provided a check for apomixis or autogamy. Seven plants were used to test for self-fertility, five at WD, and one each at L and DS. During anthesis, one domestic hive honeybee, Apis mellifera L., was introduced into each bag. Hand pollination proved to be too difficult and damaging, so this milkweed pollinator was utilized to self-pollinate the test plants. Otherwise, the plants were checked frequently, but not disturbed until flowering had ended and fruiting had begun.

The remaining 10 plants were used to determine the effectiveness of nocturnal versus diurnal pollinators. Five of the plants were unbagged and exposed for 12 periods from approximately 0830 to 1930 hours and the remaining five plants were unbagged for an equal number of periods from approximately 1930 to 0830 hours. These plants were bagged following the 12 exposure periods until flowering had ended and fruiting had begun.

Nectar: Nectar quantity was determined during morning, afternoon, and evening observation periods, using a 1.0 μl syringe graduated to 0.1 μl. All five hoods were sampled and an effort was made to withdraw all nectar, including that in the constricted hood bases. Flowers for sampling were selected somewhat at random, with preference given to those appearing to have nectar in the hoods. Care was given to cleaning and emptying the syringe to prevent inflated measurements and a sugar-frozen plunger.

Insect Visitors: Insect visitors were observed for 20 one-hour periods and collected for an additional hour following each observation period. Insect identity, number and behavior were recorded along with an estimation of pollinaria carried. Collected insects were pinned and preserved. A few were placed in Hood's solution for preservation. All insects were identified to family. Major pollinators and common insects were identified to species.

Corpuscula were assayed on the collected insects for number per specimen and site of attachment, using a stereoscopic microscope. Slides were made of pollinaria from *Asclepias incarnata* and the sympatric *A. syriaca* and *A. verticillata* for comparison and identification. Pollinaria were also assayed on representative pollinators for their condition; that is, as to whether they were intact, lacking one pollinium, lacking both pollinia, or lacking both pollinia and translator arms (Fig. 4). Records were also kept of the number of basal corpuscula (those attached directly to the insect) and distal corpuscula (those attached to the translator arms or pollinia and forming chains).

Schedule: Site visits were scheduled at approximately 0900, 1500, and 2100 hours. The site and time for an observation period were determined on a rotating basis, with one period completed per day. Site WD was visited twice each day during the 12 nocturnal-diurnal bagging exchanges. These visits to WD were often incorporated with the observation and collection periods at sites WD and L.

RESULTS AND DISCUSSION

Growth Characteristics and Habitat

The populations studied at Fontenelle Forest (FF) consisted of four plants found on June 2 in an area of open sun, in wet soil, with mixed grasses and six plants found on June 19, growing in partial shade at the extreme edge of the stream. The plants identified early in June were approximately 35 cm tall while those found later were nearly 2 m tall and had flower buds which were beginning to turn pink.

Plants examined at WD, west of Omaha, included 15 found on June 5 along the perimeter and center of a dry-land extension into open swamp and water-filled ditch. The plants were approaching 1 m in height and were restricted to a strip of wet to submerged soil in open sun, among short rushes (*Eleocharis erythropoda* Steud.).

Eight plants were observed at Desoto National Wildlife Refuge (DS). These were found on June 14 in very sandy, wet to water-covered soil, in open sun. The swamp milkweeds were less than 1 m tall, scattered rather widely apart and surrounded primarily by *Equisetum hyemale* L.

At site L, only a few plants had been found in the overgrown swampy soil to the west until June 29, when nearly 200 plants about 1.5 m tall and blooming were counted in dense concentrations east of Highway 275. These plants were most susceptible to disturbance, being on a state-maintained wet drainage area below a cornfield.

The general ecological preference of Asclepias incarnata was for wet, somewhat sandy soil in areas of open sun. These conditions were found at all four study sites, which included the edges of an open swamp (WD), a low grassy drainage area (L), the banks of a swamp/woodland stream (FF) and the margins of a water surrounded sand bar (DS). Disturbed sites had the greatest numbers and concentrations of plants, especially site L which was completely mowed on August 28, apparently a yearly occurence. All sites showed considerable variation in water level, with WD going from nearly a six-inch depth to very dry cracked soil as the weather progressed from wet spring to dry summer. The least variation in water level was at FF, possibly because of beaver activity.

Asclepias incarnata apparently began to grow in mid to late May, as evidence by 1 m tall specimens found on June 14. Many plants recurred on perennial roots, providing an easy method for locating them: after areas of likely habitat were selected, the old dried stems from previous years, which branch distinctly near the top, were easy to distinguish. By July 1, plants at WD were showing floral buds. Several plants were found to be starting anthesis by July 14. Anthesis became much more rapid and continued through August 11, when fruiting follicles (pods) began to form. Pods matured and released seed first on September 5, with dehiscence completed by October 9. Considerable variation in time of reaching 1.5 m height, anthesis, and fruiting was noted. On a single plant, the flowers opened gradually within an inflorescence and terminal inflorescences before lower ones, prolonging the flowering time to nearly four weeks.

In general, the plants at FF and DS were one week behind the disturbed sites in initiation of flowers, pods and seed release. Plants at FF and DS also produced fewer and smaller inflorescences.

Other plants identified in the *Asclepias incarnata* study sites are summarized in Table I. Considering the variability of habitat offered at each of the sites, ranging in a short space from open water or swamp through wet soil to dry ground, a wide variety of plants was found. While exhaustive plant lists were not made, it appeared that the weedy disturbed sites had a greater diversity.

The flora competing for pollinators with *Asclepias incarnata* were primarily *Lythrum dacotanum* Nieuw. at WD, *Eupatorium purpureum* L. at FF, *A. verticillata* L. and *Cassia fasciculata* Michx. at DS and *Apocynum sibiricum* Jacq. at L. Insects appeared to specialize on particular species for periods of time, with some venturing between sources of pollen or nectar.

Nectar

Nectar quantity per flower was quite variable at all three time periods, morning 0700-1100 hours, afternoon 1400-1700 hours, and evening 1800-2000 hours (Fig. 5). Often nectar was visible in the hoods, if only as a glaze, but not recoverable. Several of the largest quantities measured came predominately from a single hood, up to 1.5 µl. Nectar quantity was most dependent on flower age, being greatest early after anthesis. Similar age-dependency of nectar production has

Table I. Flora identified in *Asclepias incarnata* study sites

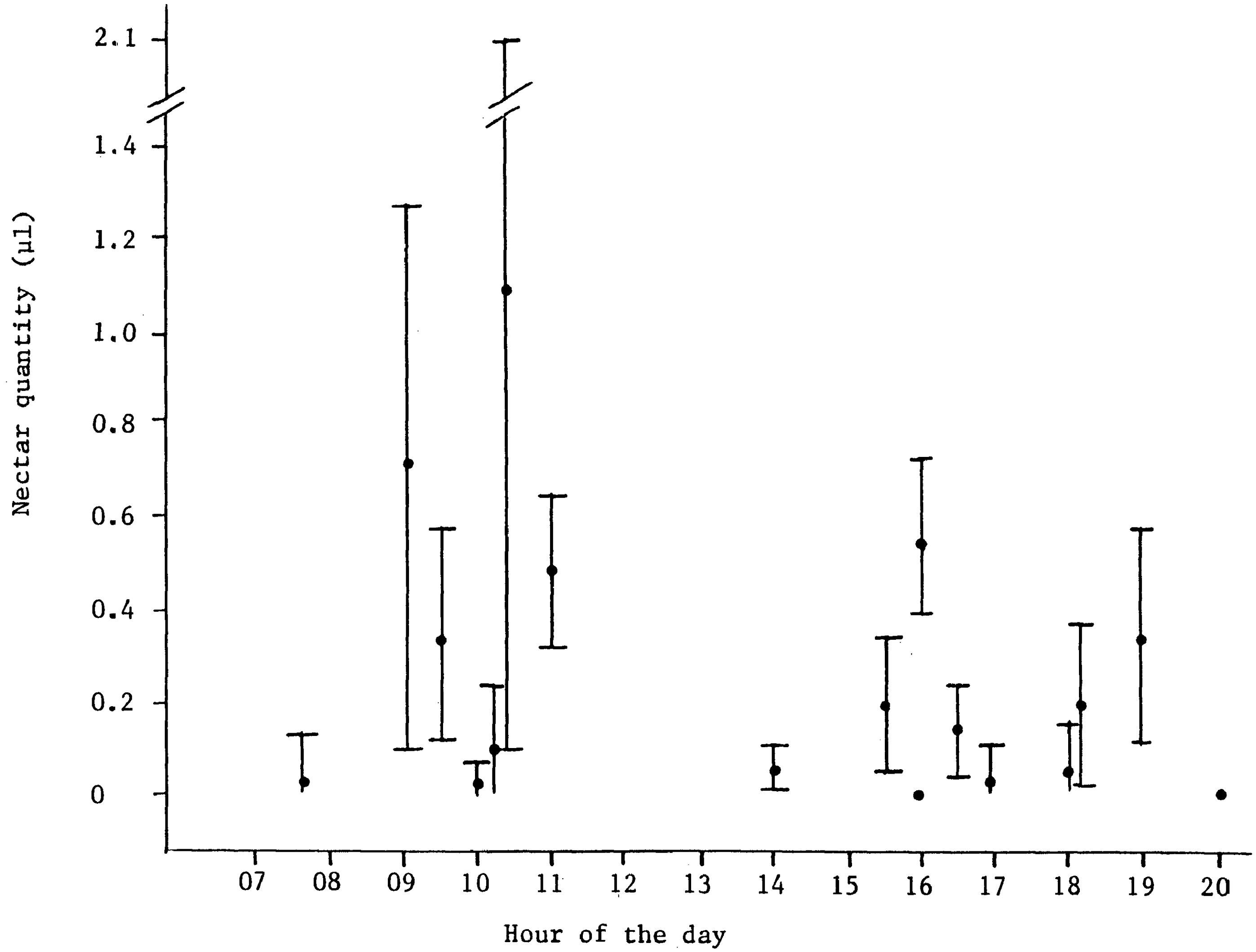
Plant	Site	Number
Lythrum dacotanum Nieuw.	WD	common
Salix interior Rowlee	WD, DS	abundant
Populus deltoides Marsh	WD	abundant
Salix amygdaloides Anderss.	WD	few
Asclepias syriaca L.	WD, DS	common
Teucrium canadense L.	WD	few
Lycopus americanus Muhl.	WD	few
Polygonum coccineum Muhl.	WD	few
Juncus torreyi Cov.	WD	abundant
Asclepias verticillata L.	WD, DS, L	common
Phyla lanceolata (Michx.) Greene	WD	abundant
Eleocharis erythropoda Steud.	WD, L	abundant
Equisetum hyemale L.	DS	abundant
Cassia fasciculata Michx.	DS	common
Verbena hastata L.	DS, WD	few
Convolvulus sepium L.	WD	few
Sagittaria latifolia Willd.	WD	few
Hibiscus militaris Cav.	WD	common
Lysimachia ciliata L.	WD	few
Alisma plantago-aquatica L.	WD	few

(continued on next page)

Table I. (cont.)

Plant	Site	Number
Erigeron strigosus Muhl.	WD	common
Cicuta maculata L.	WD	few
Typha sp.	WD, DS, L	com/abun
Melilotus alba Desr.	WD	few
Scirpus acutus Muhl.	WD, DS, L	com/abun
Salix rigida Muhl.	WD	few
Apocynum sibiricum Jacq.	WD, L	common
Thelesperma filifolium (Hook.) Gray	L	few
Silphium integrifolium Michx.	L	common
Desmanthus illinoensis (Michx.) Macmill.	L	common
Solidago gigantea Ait.	L	few
Eupatorium purpureum L.	FF	few
Desmodium canescens L.	DS	few
Oenothera biennis L.	DS	few

Figure 5. Mean nectar quantity of a flower by hour of the day. The bars show one standard deviation.



been reported for *A. syriaca* (Southwick et al. 1983). Mean nectar quantity was found to be greater in the morning (0.38 μl) than afternoon and evening levels (0.16 and 0.145 μl, respectively). A one-way analysis of variance (ANOVA) of morning/afternoon/evening nectar levels (Table II) showed significant difference ($F_{2,87} = 3.92$, $P = 0.024$). Pairwise analysis of variance showed significant difference between morning and afternoon nectar quantities ($F_{1,68} = 4.72$, $P = 0.032$) and near significant difference between morning and evening levels ($F_{1,58} = 3.79$, $P = 0.054$). No significant difference was found between afternoon and evening nectar quantities, ($F_{1,48} = 0.063$, ns). Bookman (1983) reported that *Asclepias speciosa* L. nectar content was greatest in early morning hours, and Southwick et al. (1983) found that *A. syriaca* nectar production peaked at 0800 hours; two reports consistent with the results for *A. incarnata*.

Nectar composition and equivalents of sucrose were not determined, but have been reported as almost exclusively sucrose of 35% maximum concentration for *A. verticillata* (Willson et al. 1979). The same study measured quantities of 0.7 μl from repeatedly sampled flowers, with some bagged flowers yielding single amounts of up to 2 μl. Southwick et al. (1981) reported that *A. syriaca* nectar was nearly a pure sucrose solution of 57.6% average concentration. They also measured average nectar volume per hood of 0.5 μl, with some in excess of 1.0 μl. Percival (1965) stated that nectar characteristics were often consistent throughout floral families, and *A. incarnata* was found in this study to be comparable with other local *Asclepias* species in

Table II. Analysis of variance of *Asclepias incarnata* nectar quantity in three time periods*

Time Period	Nectar Quantity (μl)	ANOVA			
	Mean ± SD	df	SS	Fs	P
Morning	.38 ± .52	Morning/Afternoon			
		69	12.77	4.72	.032
After-noon	.16 ± .22				
		Afternoon/Evening			
		49	2.06	.06	.791
Evening	.15 ± .19				
		Morning/Evening			
		59	12.01	3.79	.054
		Total Morning/Afternoon/Evening			
		87	13.77	3.92	.024

*(SD = standard deviation, df = degrees of freedom, SS = sum of squared deviations, P = probability. P is considered statistically significant here when less than or equal to 0.05.)

nectar quantity and pattern of production.

Scent

No distinct variations were noticed in floral perfume during different times of day; in fact no particular scent was noted at any time. A flat sugary fragrance was vaguely perceived infrequently, but odors from other sources in the area were much more noticeable. This was especially true in the swampier habitats late in the summer as water level receeded, when a decaying fish odor was pervasive.

Bagging Experiments

Apomixis or autogamy: The three plants used to test for apomixis and autogamy initiated 18 fruits, maturing and dehiscing five (Table III). The number of pods releasing seeds in these test plants was only 6.83% of the unbagged controls. The plant at L matured four pods to a size of six centimeters, but subsequent visits found all four damaged by insects. Only the seed fiber remained; all immature seeds were eaten. The plant at WD initiated 10 fruits, maturing four and dehiscing three of these with the fourth taken for embryo tests. Fully formed, viable embryos were found in the seeds. The third plant, at DS, had two pods dehiscing at last check. This plant had been severed approximately six inches above the soil, but the seed release appeared normal. In summary, even though covered by mesh which presumably prevented pollinator access, all three plants initiated fruits and would have released fertile seeds. It was noted on a few of the bagged

Table III. Average follicle initiation and dehiscence in plants bagged to test breeding system*

Test	n	Follicles Initiated Per Plant	Follicles Dehisced Per Plant
Apomixis or Autogamy	3	6.0 ± 2.83	1.67 ± 1.25
Self-Fertility	7	3.0 ± 3.25	1.57 ± 2.26
Nocturnal	5	11.0 ± 3.69	3.80 ± 3.19
Diurnal	5	15.40 ± 8.52	6.80 ± 6.76
Controls at FF	4	35.25 ± 5.80	33.75 ± 3.77
Controls at WD	9	25.55 ± 7.97	20.33 ± 10.26
Controls Total	13	28.54 ± 8.63	24.46 ± 10.75

*The values represent the mean ± one standard deviation.

plants that these pods were somewhat lighter green and seemed to develop late in the season. The significance of this was unclear, but it was thought possible that lacking pollination, plants may have initiated follicles by apomixis or autogamy.

Self-Fertility: The seven plants manipulated for self-fertility testing initiated an average of three fruits per plant with approximately 1.57 pods per plant releasing seeds (Table III). This was only 6.42% of follicles of unbagged control plants. Again, the plant at L produced follicles only to have insects breach the pods and destroy the embryos. The plant at DS had seven pods of 5 cm length in mid-October, but these were yet green and several days or more from opening. Of the five plants at WD, two were decimated by aphids. Both had flowers and fruit, but aborted all whan an extensive aphid infestation occurred. One additional plant at WD aborted all reproductive effort. This third plant had many, heavy inflorescences when the honeybee, Apis mellifera L., was introduced into the bag. Growing in considerably drier ground, with much more apparent competition, this plant suffered damage due to wind and the weight of the inflorescences. Despite being staked, several of the inflorescence branches were bent and by mid-August flowers were being dropped. This continued until only vegetation remained. The plant further declined. wilting and becoming discolored, suggesting the additional factor of water stress.

Of the remaining two self-fertility test plants at WD, one produced a single pod which dehisced normally, and the final plant initiated nine fruits with four dehiscing and the others varying between green (two), to wilted (two), to black (one) at final visit. The introduced hive honeybees did forage the flowers and move pollinaria. An assay of two of these (Table IV, page 33) showed eight basal and eight distal corpuscula on the tarsal claws and 20 basal and eight distal corpuscula on leg hairs. These counts compare well with those of unrestrained *Apis mellifera*.

Asclepiads are thought to be dependent upon insect vectors for pollination and fruit production, with apomixis, autogamy and self-fertility not prevalent. The results obtained here indicate either a procedural problem or a possibility of apomixis, geitonogamy, or autogamy for *A. incarnata*. Although apomixis and autogamy have received little previous consideration, Kephart (1981) found a 29.2% rate of success for artificially manipulated intraspecific self-pollinations in *A. incarnata*, as compared with 0% for *A. verticillata*, and 4.2% for *A. syriaca*. Bumblebees at WD were observed on bagged plants foraging, or at least attempting to forage for nectar and potentially pollinating the flowers. Although it seems unlikely, the legs may have reached through the mesh far enough to withdraw pollinaria and deposit pollinia. The tarsal claws of the bumblebees, at a maximum width of approximately 1.0 mm, could have just fit through the mesh. The body weight of the bumblebees was sufficient to press the mesh across the inflorescences, further reducing the distance necessary for the leg to pass through the openings. While possible that external pollinators may have contaminated these samples, it is still held unlikely, and at least the self-pollination results obtained here were corroborated by Kephart (1981). The levels of self-fertility and apomixis or autogamy apparently found here, while low, indicate at least a possibility that these plants can produce seed without pollinator activity.

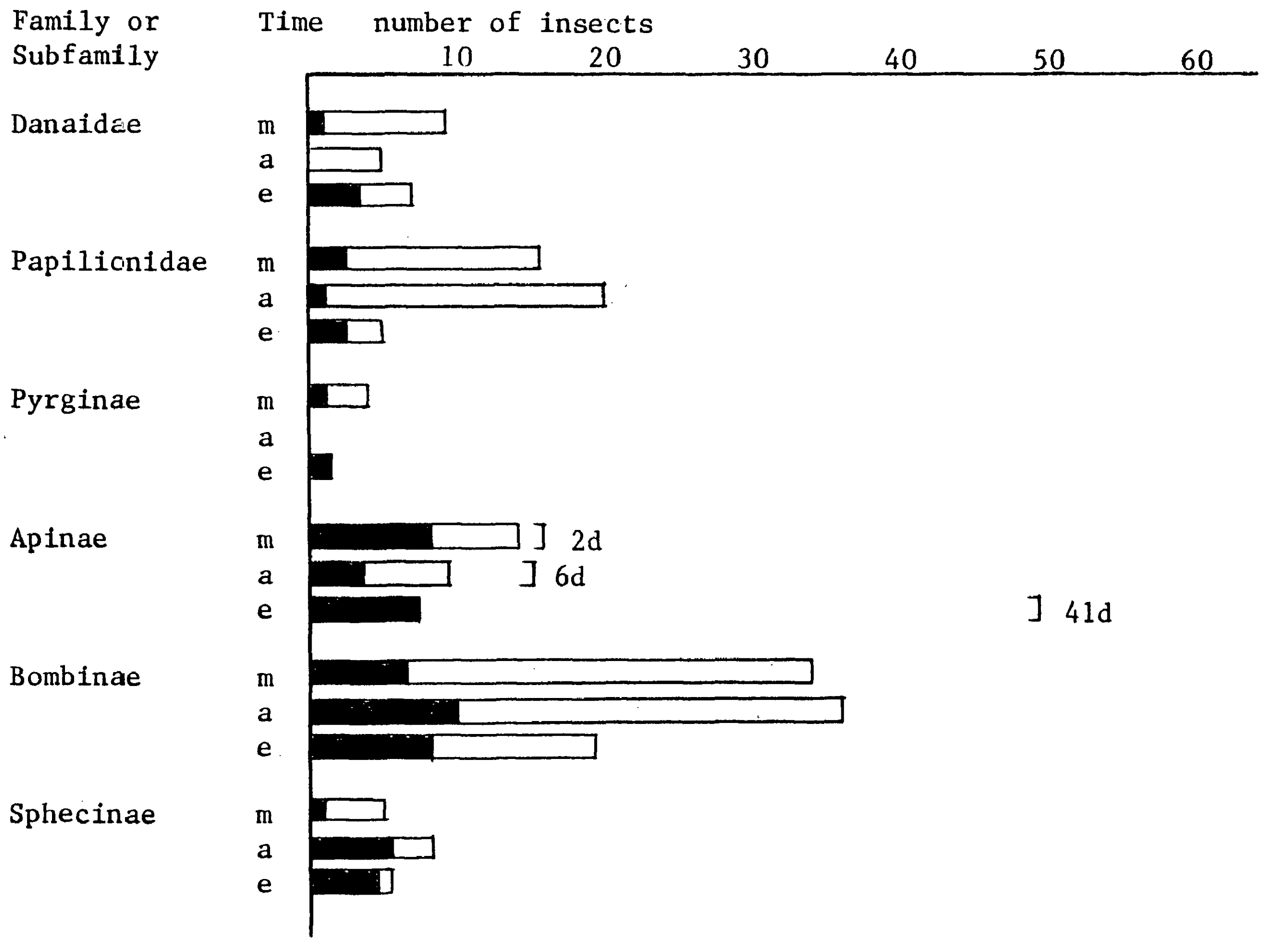
Diurnal versus nocturnal pollination: Bertin and Willson (1979) stated that nocturnal pollinators of *Asclepias syriaca*, though less frequent and removing and inserting fewer pollinia, caused more seed set than diurnal pollinators, possibly due to behavior patterns, climatic factors, or nectar quantity in the stigmatic chambers. The five nocturnally exposed *A. incarnata* plants at WD dehisced 15.5% and the five diurnally exposed plants dehisced 27.8% of the number of pods dehisced in the controls (Table III). Aphids and other insects damaged and reduced seed number in these plants, decimating one and considerably reducing the reproductive effort of nearly half of the others. Physical handling of these plants during the bagging and unbagging may have further reduced fruit production. The insects collected after 2000 hours were entirely moths and carried few pollinaria, almost all intact (Table IV, page 31). The sphinx moth, *Hyles lineata* (Fabricius), the largest and most common moth, well known as a pollinator of long-tubed flowers, showed little evidence of pollination activity here. This moth rarely landed on the inflorescence, instead hovering near and probing the hoods with its long proboscis. Complicating this nocturnal versus diurnal pollinator distinction, at least experimentally, was the overlap of times of visitor occurrence. The bees were found to be active very early in the morning and late into the evening. The possible problem with pollinator exclusion and/or apomixis or autogamy further clouded these results. Beyond these difficulties, much more insect activity was evident during daylight hours (Fig. 6), and diurnal insects carried more pollinia (Table IV, page 31).

Other Observations

It was also noted that plants at FF produced 38.0% and dehisced 66.0% more pods than the plants at WD (Table III). This might have been due to a more constant resource supply, as in the previously discussed water level, or a difference in pollinator success as suggested by Bertin and Willson (1980).

It has been reported that pod production is milkweeds is not limited by pollinators, but rather by energy or nutrients (Willson and Price 1977, Willson and Price 1980). Such resource limitation and selective fruit abortion (Bookman 1983) would seem to reduce the significance of any differences among the effectiveness of particular pollinators. Also, if apomixis or autogamy occurs in _A. incarnata_, then even without pollinator activity, a plant could set a small number of follicles for seed dispersion.

Figure 6. Major pollinators collected (closed portion of bar) and observed (open portion of bar) by time period. The abbreviations are: m = morning (0700-1100 hours), a = afternoon (1200-1700 hours), e = evening (1800-2000 hours), and the (d) refers to insects found dead.



Flower Visitors

Insects from 25 families within five orders were observed and collected on Asclepias incarnata (Fig. 7). Among the first visitors noted were those for which this milkweed serves as a food source. Three Coleopteran species of subfamilies Chrysomelinae, Cassidinae, and Lamiinae, all of which utilize this plant as an adult food source, were common throughout the growing year. These beetles were never present in abundance and were not apparent causes of major plant damage. Their common names, swamp milkweed beetle, milkweed tortoise beetle, and red milkweed beetle, respectively, indicate the typical association of these insects with Asclepias species (Milne 1980). The larvae of the milkweed butterfly, Danaus plexippus (L.), order Lepidoptera, was a much more destructive herbivore. Though not especially numerous, they caused considerable defoliation on afficted plants.

Several families of the Order Hemiptera were observed and collected during the growing season. The small eastern milkweed bug (Lygaeidae) was often found feeding on the plants, but never in abundance. A stink bug, family Pentatomidae, was collected on as A. incarnata, but no apparent relationship existed between the two organisms. The other Hemipteran species collected and observed, an ambush bug of the family Phymatidae, was common at L and abundant at WD. These predators, often several in a single inflorescence, captured other insects with their much developed prothoracic legs and, by means of piercing mouthparts, punctured the exoskeleton and withdrew the body fluids. Over a two week period, an average of five dead honeybees were

Figure 7. Insects collected (closed portion of bar) and observed (open portion of bar). The (d) refers to insects found dead.

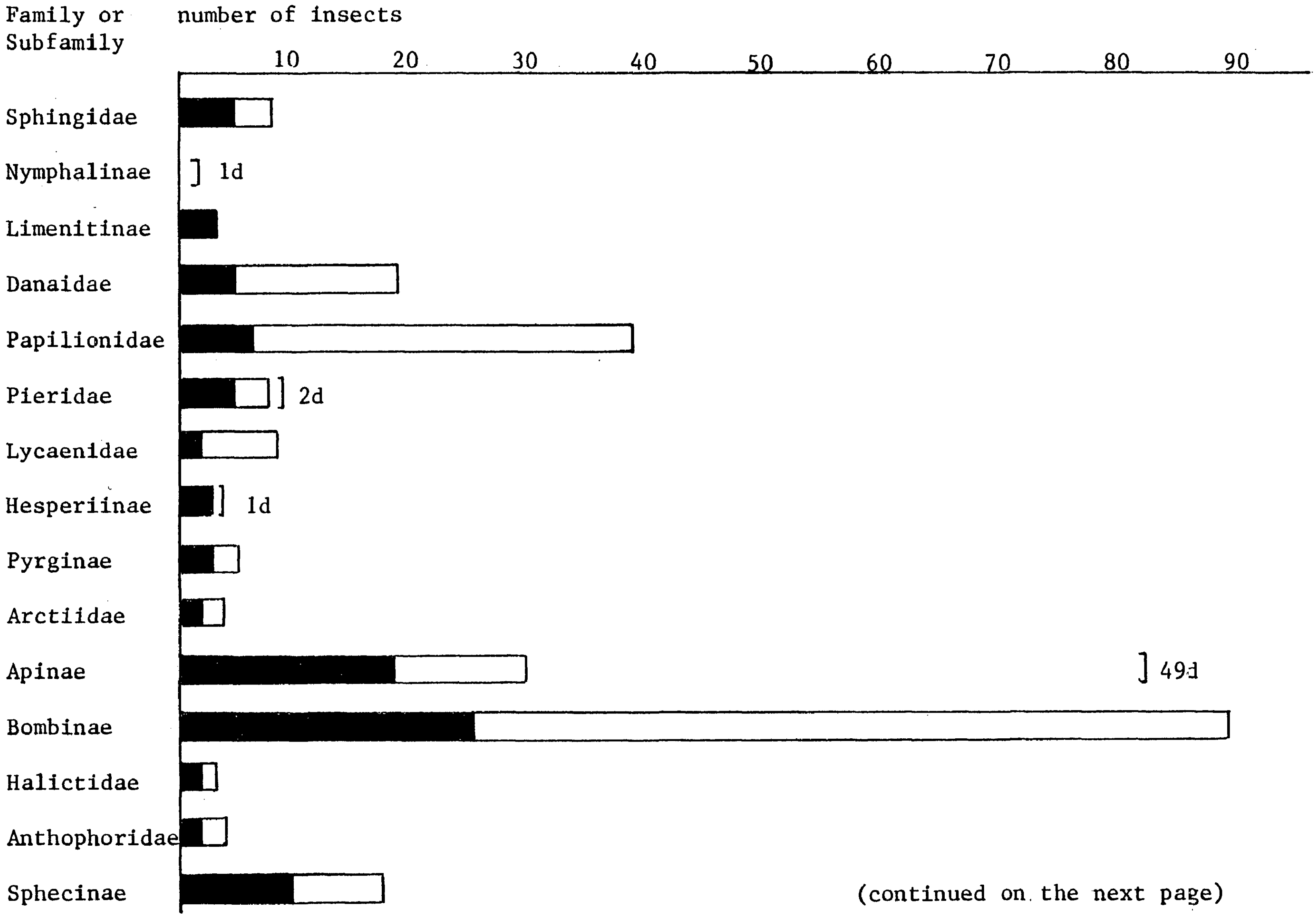


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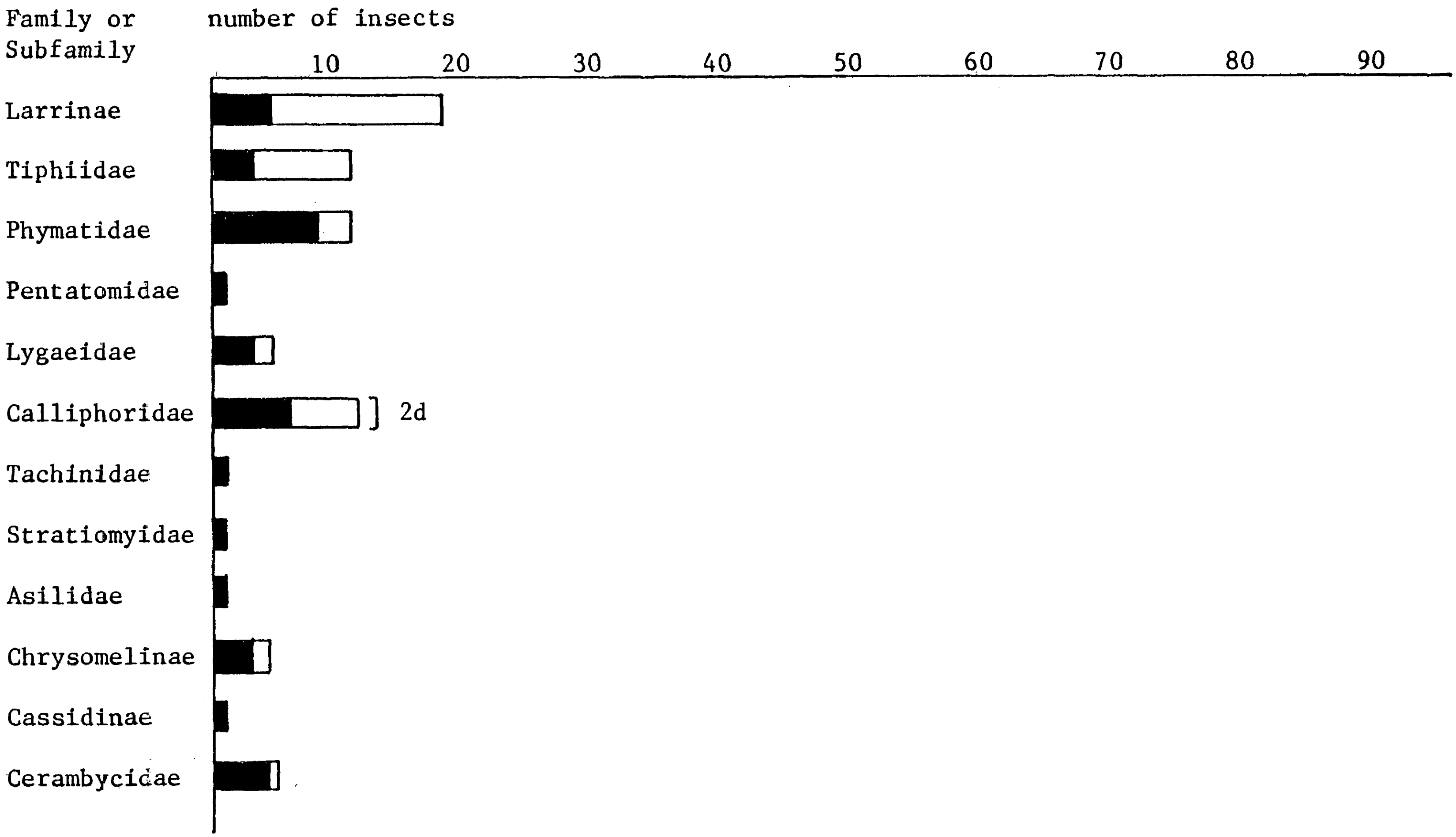
Figure 7. (cont.)



found per day hanging from approximately 10 plants, each bee often still held by a Phymatid. Sulfur butterflies, Colias spp., and even an infrequent Monarch butterfly, Danaus plexippus, were victims of this small (1 cm) insect.

Other predators of milkweed pollinators were robber flies (Order Diptera, Family Asilidae) and spiders (Order Araneae). One particular spider, a small green species, waited in ambush within the inflorescence, much as the Phymatids did. It is very unlikely that pollination was reduced by the loss of individual pollen vectors, since pollinators occurred in such large numbers and the dead bees showed considerable evidence of previous successful activity. In addition, dead honeybees were almost exclusively found in the evening, whereas activity of Apis mellifera was greatest in the morning (Fig. 6). Nevertheless, the presence of a dead insect on an inflorescence would seem likely to deter nectar foraging by conspecific insects, though no observations of this were made.

The pollen of Asclepiads, in the cohesive pollinial masses, is not an attractant to insects, being instead almost a deterrent, since it causes certain foraging difficulties (Morse 1981), and possibly contributes to their death by predator capture. It has been commonly suggested that only the larger insects successfully remove pollinaria and that small insects may become trapped with a leg stuck in the corpusculum and unable to withdraw the pollinarium. Several examples of small trapped Coleoptera (Family Phengodidae) were collected.

The copius nectar, a concentrated sugar source, is the sole and openly offered attractant. The open nature of its presentation invites nectar thieves. All insects that visit the inflorescences risk attachment of corpuscula, so a distinction was made for the purposes of this study between those with relatively few and largely intact pollinaria versus those with chains of distal and mostly incomplete pollinaria. The former were considered nectar thieves while the latter showed clear evidence of repeated foraging with pollinaria removals and probable pollinations. Some question arose as to the rate of breakage suffered by withdrawn and attached pollinaria versus the rate of successful insertions and pollinations. It was thought probable that not all pollinia broken off the translator arms would represent pollinations, so the presence of distal corpuscula was considered more indicative of pollinator success. Macior (1965) recorded basal and distal corpuscula, providing the model for this distinction. As a pollinium lodges in the stigmatic fissure its translator arm may enter and attach to the corpusculum above the fissure, which also supports this emphasis on the importance of distal corpuscula. It has been suggested that pollinia present in the anthers increase the likelihood of successful insertions. The presence of the corpusculum at the top of the alar fissure may exert leverage or tension against the translator arm promoting its separation from the pollinium (Wyatt 1976, Beare 1981). This arrangement of structures also would suggest a subsequent withdrawal of the pollinarium and formation of distal chains.

Dipteran families Calliphoridae, Stratiomyidae and Tachinidae were collected and observed, but only the metallic colored Calliphorid blowflies were common. Of these, seven specimens were collected, but only one carried a pollinarium, which was intact. The Dipterans were apparently nectar thieves. More Dipterans were found at WD, with almost no representatives of this order found at FF and DS (Appendices 1 and 2). This was also true of the Coleoptera and Hemiptera.

The Order Lepidoptera was represented by the most families, but most species appeared to be nectar thieves. Of the species identified, the Papilionidae, in particular Papilio glaucus L., were clearly pollinators. The swallowtail butterflies were observed at all sites, but only FF had a high concentration relative to the number of plants (Fig. 7). Papilio glaucus had the highest number of distal corpuscula for the butterflies (Table IV), with approximately 50% of all pollinaria missing both pollinia, 29% missing one pollinium, and 21% intact (Table V).

The silver spotted skipper, Epargyreus clarus (Cramer), (Family Hesperiidae, Subfamily Pyrginae), had the highest average corpusculum count per butterfly, but nearly 50% of these were corpuscula of intact pollinaria and very few were distal. Considering the relative infrequency of these insects (only four collected and observed) and their low percentage of indicated pollinations, the skippers were comparatively insignificant pollinators at L. Conversely, at FF or DS, with the few plants present, these insects become more important, but still not rivalling the swallowtails.

The other butterfly which has possible importance as a pollinator is the monarch, Danaus plexippus (Family Danaidae). As previously

Table IV. Assay of *Asclepias incarnata* corpuscula on collected insects

The corpuscula were recorded as basal (B) and distal (D). *A. syriaca* pollinia are indicated by (a) and *A. verticillata* by (b), beside the numerals. The (i) indicates intact pollinaria.

Insect Family or Subfamily		Sphnigidae	Nymphalinae	Limenitinae	Danaidae	Papilionidae	Pieridae
n		4	1	2	4	5	4
Tarsal Claw	B	.	.	.	.	12	1i
	D	.	.	.	.	37	.
Arolium	B	.	2a	.	.	.	.
	D	.	1a	.	.	.	.
Mouth Parts	B	.	.	1	.	.	.
	D	.	.	.	.	.	.
Leg Hairs, Spines	B	3i	.	6	12	12	2i
	D	.	.	.	4	3	.
Corbicular Pollen							
Total Corpuscula		3	3a	7	16	64	3
Mean		0.75		3.50	4	12.8	0.75
Standard Deviation		1.30		3.50	2.55	12.94	1.30

(continued on next page)

Table IV. (cont.)

Insect Family or Subfamily		Lycaenidae	Hesperinae	Pyrginae	Arctiidae	Apinae live	Apinae dead
n		1	3	2	1	18	9
Tarsal Claw	B	.	.	.	1i	54	35, 2a
	D	.	.	.	1i	73	42, 5a
Arolium	B	.	.	.	.	22, 34a	11, 21a
	D	.	.	.	.	72, 8a	50, 6a
Mouth Parts	B	.	.	.	.	18, 4a	6, 2a
	D	.	.	.	.	27, 1a	4
Leg Hairs, Spines	B	.	1b	22	.	161	91, 1a
	D	.	1b	6	.	66	41, 1a
Corbicular Pollen							1
Total Corpuscula		0	2b	28	2	495, 47a	280, 38a
Mean				14.0	2.0	27.5	31.11
Standard Deviation				5.0	2.0	17.87	21.15

(continued on next page)

Table IV. (cont.)

Insect Family		Apinae	Bombinae		Sphecinae*		Larr-	Tiphi-
or Subfamily		sf*	P*	M*	1 spp.	2	inae	idae
n		2	11	13	7	3	5	5
Tarsal Claw	B	8	2	15	1	3	.	1
	D	8	.	33	.	3	.	3, 2a
Arolium	B	.	.	1	9a	3a	.	.
	D	.	.		1	2	.	.
Mouth Parts	B	.	1	24	1	1	.	.
	D	.	.	37	2	4	.	.
Leg Hairs, Spines	B	20	69	813	161	193	20	10
	D	8	10	372	23	47	1	.
Corbicular Pollen				2				
Total Corpuscula		44	82	1295	189, 9a	253, 3a	21	14, 2a
Mean		22.0	7.45	99.6	27.0	84.33	4.20	2.8
Standard Deviation		1.0	5.37	28.72	16.16	59.23	6.08	3.06

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*sf represents the self-fertility-test honeybees. M indicates the Megabombus pennsylvanicus and P the Pyrobombus griseocollis. Sphecinae species 1 was tentatively identified as Sphex ichneumoneus L. and species 2 was an unidentified common blue-black wasp.

(continued on next page)

Table IV. (cont.)

Insect Family or Subfamily		Anthophoridae	Halictidae	Phymatidae	Pentatomidae	Lygaeidae	Calliphoridae
n		1	1	8	1	3	7
Tarsal Claw	B	.	.	.	.	.	.
	D	.	.	.	.	.	.
Arolium	B	.	.	.	.	.	.
	D	.	.	.	.	.	.
Mouth Parts	B		.	.		.	
	D		.	.		.	
Leg Hairs, Spines	B		.	.	.	.	1
	D		.	.	.	.	
Corbicular Pollen							
Total Corpuscula		0	0	0	0	0	1
Mean							0.14
Standard Deviation							0.35

(continued on next page)

Table IV. (cont.)

Insect Family or Subfamily		Tachinidae	Stratiomyidae	Asilidae	Cassidinae	Chrysomelinae	Lamiinae
n		1	1	1	1	3	4
Tarsal Claw	B	.	.	.	.	.	.
	D	.	.	.	.	.	.
Arolium	B	.	.	.	.	.	.
	D	.	.	.	.	.	.
Mouth Parts	B	.	.	.	.	.	.
	D	.	.	.	.	.	.
Leg Hairs, Spines	B	.		.	.	.	.
	D	.		.	.	.	.
Corbicular Pollen							
Total Corpuscula		0	0	0	0	0	0
Mean							
Standard Deviation							

Table V. Pollinaria condition on collected pollinators; proportion of total number of corpuscula assayed*

Pollinator Family, Subfamily, or Genus	n	Corpusculum Only	Corpusculum and Translator Arms	Lacking One Pollinium	Intact	Distal
Danaidae	4	.	.125	.437	.438	.250
Papilionidae	3	.	.50	.286	.214	.464
Pyrginae	2	.036	.214	.250	.50	.214
<u>Apis</u> (live)	3	.	.376	.271	.353	.435
<u>Megabombus</u>	3	.040	.558	.182	.219	.223
<u>Pyrobombus</u>	3	.086	.429	.143	.343	.057
Sphecinae** species 1	3	.	.452	.190	.357	.071
species 2	2	.	.494	.271	.235	.176

* The first four columns of proportions should total to 1 in each case.

**Sphecinae species 1 was tentatively identified as Sphex ichneumoneus L. and species 2 was an unidentified common blue-black wasp.

mentioned, the larvae of the monarch feed on this plant and can do considerable damage. The adults are attracted by the nectar, but appear to do little for the plant in return. A distinct difference was noted between the foraging behaviors of the monarch and swallowtail butterflies. The swallowtails, as previously noted by Robertson (1887), had frequent leg movements and constant forewing fluttering. The monarchs were much more controlled in their movements with slower leg movements and motionless wings. This distinction may explain the observed lower rate of pollinaria removal by the monarchs. On the four monarchs collected, there were a total of 16 corpuscula; 12 of these were basal and six distal. Of the 12 basal, four had both pollinia, seven were lacking one pollinium, and one had only translator arms but carried a chain of four distal corpuscula (Table IV). The swallowtails had approximately 50% corpuscula lacking both pollinia, versus only 12% for the monarchs. The monarchs also showed many more intact pollinaria (44%) and fewer distal corpuscula (25%) than the swallowtails, 21% intact and 46% distal (Table V). The monarchs then, observed at all four sites and in fair numbers, were not significant pollinators at WD and L. They were more important at FF and DS, only because they constituted a larger percentage of the low pollinator numbers at these sites.

The other Lepidopterans observed and collected on A. *incarnata*, carried few and mostly intact pollinaria, and were not frequent visitors (Fig. 7). These nectar thieves were mostly smaller than the pollinators, which may or may not have affected their pollinaria removal rate. Notable among these was the nocturnal sphinx moth, *Hyles lineata*, which presented no evidence of successful pollinations. Four specimens were collected as they foraged for nectar, but only one bore pollinaria, all three of which were intact. Also of note was the Nymphalid brush-footed butterfly, commonly called the American painted lady, because the one specimen collected carried three *Asclepias syriaca* corpuscula with one of these having both pollinia intact. One skipper (Subfamily Hesperiinae) collected at DS, carried two *A. verticillata* corpuscula (one with both pollinia and the other lacking one pollinium) reflecting the close proximity and common occurrence of *A. verticillata* at this site (Tables I and IV).

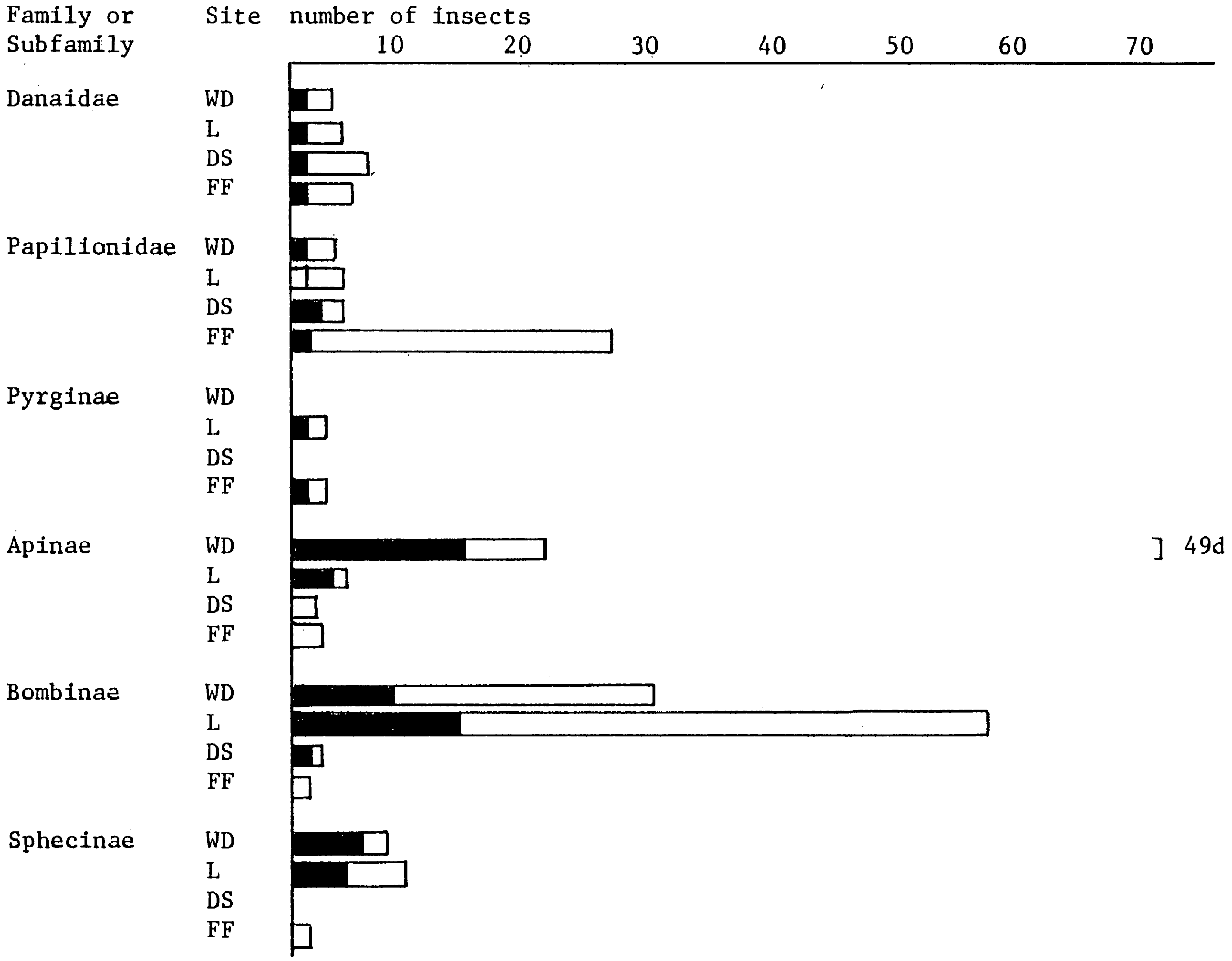
The order Hymenoptera, represented by 185 observed and live collected specimens from six families, was the most abundant insect group and included the most important *Asclepias incarnata* pollinators. The introduced European honeybee, *Apis mellifera*, was the first pollinator encountered, and it occurred in comparatively large numbers (Table IV, Appendices 1 and 2). Initial observations of honeybees were made as they foraged early flowers on July 21 and the following days. They continued to be common until early August, at which time the bumblebees became numerous. Eighteen live honeybees were collected and 12 observed as they worked flowers. In addition, 49 dead honeybees were collected, almost exclusively from Phymatid ambush bugs, and predominantly in the evening, as mentioned previously. The dead honeybees represent separate and longer "collection" periods than the other insects, so they were treated separately in this analysis.

All 49 dead honeybees, 14 of the live collected and seven of the observed were from WD (Fig. 8). The largest concentration of plants at L was not located until very late July and few honeybees were encountered there. Few honeybees were seen at FF or DS.

As previously reported by Macior (1965), honeybees carried most of the corpuscula on leg hairs. Many corpuscula were attached to the tarsal claws and arolia and most bees had a few attached to the mouth parts, primarily the labial palps (Table IV). It has commonly been suggested that honeybees make few interspecific flower visits, instead specializing during bloom to a single species with sufficient nectar flow. The common occurrence of *Asclepias syriaca* corpuscula on the arolia did not necessarily support this suggestion, unless they had remained attached for a long period of time, during which the bees had changed primary nectar sources. This long-term attachment is supported by the condition of the pollinaria, since approximately 65% of them were present only as the corpusculum without pollinia or translator arms. Intact *A. syriaca* pollinaria and corpuscula with one pollinium were found on honeybees, but infrequently. In comparison, more *A. syriaca* corpuscula were found attached to the arolia than *A. incarnata* corpuscula, even though *A. syriaca* corpuscula represented less than 10% of those assayed on all honeybees, live or dead (Table V).

The honeybees were early and definite pollinators, with an average of 38% of the corpuscula lacking both pollinia and 43% of them distal. Only the swallowtails had more distal corpuscula, but they were not

Figure 8. Major pollinators collected (closed portion of bar) and observed (open portion of bar) by site. Abbreviations are from the text, page 6, and (d) refers to insects found dead.



common until early August and only at FF. The bees collected dead had a slightly higher average corpusculum count, 31.1 versus 27.5 for the live collected bees, but the variation within both groups was considerable (Tables IV and V).

The most abundant pollinators were the bumblebees, Subfamily Bombinae (Fig. 7). Two species were identified, Pyrobombus griseocollis (DeGeer) and Megabombus pennsylvanicus (DeGeer) (Milliron 1971, 1972, 1973). The occurrence of the two species overlapped, but M. pennsylvanicus was more common after August 5 with P. griseocollis before this. The bumblebees were common from early August at site L where 14 specimens were collected and 42 observed. WD had many bumblebees, with nine collected and 20 observed. DS had few of these pollinators, one observed and one collected. FF had only one bumblebee observed, which briefly circled an inflorescence and flew away.

Pyrobombus griseocollis, smaller and less brightly colored, carried an average of only 7.45 corpuscula. Of these, only 6% were distal, but 42.8% were minus both pollinia (Tables IV and V). In a surprising contrast, the Megabombus pennsylvanicus carried an average of 99.6 corpuscula per insect with 22% distal and 56% missing both pollinia. Three of these larger and more brightly yellow bumblebees had over 140 corpuscula attached to their legs and mouthparts.

As Macior (1965) reported, corpuscula attached most frequently to the leg hairs in Bombinae. In this study, they were almost exclusively so attached in P. griseocollis. In addition, in M. pennsylvanicus, corpuscula were also attached to tarsal claws and mouth parts, especially the latter (Table IV).

The identification and separation of these bumblebees into the two species was complicated by the range of variation found. The most consistent identifying characters were the length of the malar space and the color of the third abdominal tergum. Yet, when compared with the corpusculum assay, the division became clear, as P. griseocollis carry so few corpuscula compared to M. pennsylvanicus. While being the second largest group of insects collected, exceeded only by Apis mellifera, M. pennsylvanicus was the most important pollinator at L and WD, where A. incarnata occurred in abundance. At sites FF and DS the bumblebees were insignificant or entirely absent.

Also of interest was the pure occurrence of A. incarnata corpuscula on the Bombinae, which are reported to exhibit less floral constancy than the honeybees. Here, the opposite was found. Of the 24 Bombinae collected, only two carried other pollen (Table IV).

Ten insects of the Subfamily Sphecinae, solitary wasps, were collected. Seven of these were tentatively identified as Sphex ichneumoneus L., the common great golden digger wasp. The other three were of a dark blue-black species and were not identified. The golden wasps carried an average of 27.0 corpuscula and the darker wasps carried approximately 84.3 corpuscula each. One blue-black wasp had 168 corpuscula attached to its legs. Again, as previously reported by Macior (1965), the wasps carried corpuscula on their leg spines with very few on the arolia or mouthparts (Table IV). These two species had 7% and 18% distal corpuscula, respectively, and 45% and 49% corpuscula missing both pollinia (Table V). Though not present in large numbers at WD and L, these insects served as pollinators of some importance. They were not seen at DS and only one specimen of the blue-black wasp was observed at FF, and it did not land after circling the inflorescences several times. This behavior was typical of the Sphecinae, which flew over what appeared to be relatively long distances, circled many inflorescences and landed on few. When foraging the flowers for nectar, these large insects were very active with rapid movements, but they were easily disturbed and did not return to the inflorescence.

Twelve *Asclepias syriaca* corpuscula were found on four of these wasps, but as on the *Apis mellifera*, over half were only the corpusculum with most of the others having only translator arms. Thus, it appeared on these insects, as on the honeybees, that the *A. syriaca* corpuscula had been on the arolia for some time, likely attached before *A. incarnata* foraging (Table V).

The two final species of wasps collected were Sphecid wasps of Subfamily Larrinae and Family Tiphiidae. The Larrinae were medium sized dark-colored wasps found at all four sites. Very easily disturbed and not often seen foraging, these wasps were probably not pollinators. They typically circled the inflorescences several times with infrequent and brief foraging stops. The five specimens collected carried 21 corpuscula, of which 13 had both pollinia and four were missing one pollinium. The Tiphiidae were first noticed at WD massing on a few *Juncus torreyi* plants. Several days later, a few were found foraging for nectar. The three specimens collected had 14 corpuscula, including nine with both pollinia, two lacking one pollinium and three lacking both pollinia. One specimen carried two *A. syriaca* corpuscula, one with both pollinia and one with only the corpusculum. These insects, found only at WD, had very short legs, likely reducing their chances of withdrawing pollinaria. Even at this site, they were not considered important pollinators.

Two additional Hymenoptera were collected and observed on or near *A. incarnata*. Halictid bees were foraging for nectar at DS, but the collected specimen carried no corpuscula on its small body. Anthophorine bees were noted at L after August 16, but they were working recently opened thistle blooms and, as would be expected, were not found to be carrying corpuscula.

The final insect groups needing comment were ants and aphids. Both may have hindered reproductive success of *A. incarnata*, the ants by nectar thieving and the aphids by removing plant sap and thus removing needed resources from the flowers and any potential fruits. The ants were noted in abundance only at WD. The aphids were abundant at WD and FF. They were found at L and DS, but not in such infestations affecting multiple plants. The aphids severely reduced fruit production on many plants, decimating several. The ants had much less effect, neither being as consistently present nor apparently reducing pollinator attraction as much as might have been expected.

Summary of Flower Visitors

Several general trends were noted in insect distribution and activity from site to site. Sites FF and DS had many fewer insect families present (Fig. 8, Appendices 1 and 2), fewer *Asclepias incarnata* specimens and a lower degree of plant diversity. The weedy sites, WD and L, showed greater diversity of insects and plants, and larger populations of *A. incarnata*. The insects were less abundant later in the day and evening at all sites (Fig. 6), corresponding to the apparent pattern of nectar production, though many other factors may be cited, perhaps even the afternoon rise in temperature. The undisturbed sites had primarily butterfly pollinators. The butterflies were observed to be much more erratic in foraging and flight, usually moving some distance between attempts to forage, bypassing many plants. The Hymenopterans, particularly the bees, were much more consistent foragers, moving from inflorescence to inflorescence and plant to plant. When disturbed or having fallen off, as after trying to free a leg, honeybees or bumblebees often returned to the same inflorescence. The Sphecid wasps played much the same role as the butterflies; they moved pollinaria over greater distances, thus perhaps increasing the degree of outbreeding.

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Appendix 1. Insects collected, by date, with time and site

Date	Time	Site	Insect Family or Subfamily					
			Sphingidae	Nymphalidae	Limenitinae	Danaidae	Papilionidae	Pieridae
July								
21	1900	WD	.	.	.	.	.	.
24	1900	WD	.	.	.	.	.	.
25	1930	WD	.	.	.	.	.	.
26	0900	WD	.	1d	.	.	.	.
26	1930	WD	.	.	.	.	.	.
27	1915	WD	.	.	.	1	.	.
28	1930	WD	.	.	.	.	.	.
28	2000	L	.	.	.	1	.	1d
29	1000	L	.	.	.	.	1	.
29	2000	WD	.	.	.	.	.	.
30	2030	WD	2	.	.	.	.	.
31	0930	FF	.	.	.	.	.	.
31	2000	WD	.	.	.	.	.	1d
August								
1	1600	L	.	.	1	.	.	.
3	1630	WD	.	.	.	.	.	.
3	1800	L	2	.	.	.	.	.
4	0915	WD	.	.	.	.	.	.
6	1630	WD	.	.	.	.	1	.
7	1800	DS	.	.	.	1	2	.
8	0930	FF	.	.	.	1	1	1
8	1930	WD	.	.	.	.	.	.
10	2000	L	.	.	.	.	.	.
11	1100	L	.	.	.	.	.	1
12	1530	WD	.	.	.	.	.	.
15	1000	DS	.	.	1	.	.	.
17	1400	L	.	.	.	.	.	.
Total Collected			4	1d	2	4	5	2, 2d

(d) were insects found dead

(continued on next page)

Appendix 1. (cont.)

Date	Time	Site	Insect Family or Subfamily					
			Lycaenidae	Hesperiinae	Pyrginae	Arctiidae	Apinae	Bombinae
July								
21	1900	WD	.	.	.	.	1, 1d	.
24	1900	WD	.	.	.	.	5, 5d	1
25	1930	WD	.	.	.	.	6d	.
26	0900	WD	.	.	.	.	5, 2d	.
26	1930	WD	.	1d	.	.	2d	.
27	1915	WD	.	.	.	.	8d	1
28	1930	WD	.	.	.	.	3d	.
28	2000	L	.	.	.	.	.	.
29	1000	L	.	.	.	1	2	3
29	2000	WD	.	.	.	.	8d	.
30	2030	WD	.	.	.	.	6d	.
31	0930	FF	.	.	1	.	.	.
31	2000	WD	.	.	.	.	6d	.
August								
1	1600	L	1	.	.	.	1	5
3	1630	WD	.	.	.	.	6d	.
3	1800	L	.	.	.	.	.	2
4	0915	WD	.	.	.	.	1	1
6	1630	WD	.	.	.	.	2	3
7	1800	DS	.	.	.	.	.	.
8	0930	FF	.	.	.	.	.	.
8	1930	WD	.	.	.	.	.	.
10	2000	L	.	.	1	.	1	3
11	1100	L	.	.	.	.	.	1
12	1530	WD	.	2	.	.	.	2
15	1000	DS	.	.	.	.	.	1
17	1400	L	.	.	.	.	.	.
Total Collected			1	2, 1d	2	1	18, 49d	24

(continued on next page)

Appendix 1. (cont.)

Date	Time	Site	Insect Family or Subfamily Halictidae	Anthophoridae	Specinae	Larrinae	Tiphiidae	Phymatidae
July								
21	1900	WD	.	.	.	.	.	3
24	1900	WD	.	.	.	.	.	1
25	1930	WD	.	.	.	.	.	.
26	0900	WD	.	.	.	.	.	4
26	1930	WD	.	.	.	.	.	.
27	1915	WD	.	.	1	.	.	.
28	1930	WD	.	.	.	.	.	.
28	2000	L	.	.	.	.	.	.
29	1000	L	.	.	.	.	.	.
29	2000	WD	.	.	.	.	.	.
30	2030	WD	.	.	.	.	.	.
31	0930	FF	.	.	.	.	.	.
31	2000	WD	.	.	.	.	.	.
August								
1	1600	L	.	.	1	1	.	.
3	1630	WD	.	.	.	.	.	.
3	1800	L	.	.	2	.	.	.
4	0915	WD	.	.	.	1	.	.
6	1630	WD	.	.	1	.	3	.
7	1800	DS	1	.	.	1	.	.
8	0930	FF	.	.	.	.	.	.
8	1930	WD	.	.	.	.	.	.
10	2000	L	.	.	1	1	.	.
11	1100	L	.	.	1	.	.	.
12	1530	WD	.	.	3	1	.	.
15	1000	DS	.	.	.	.	.	.
17	1400	L	.	1	.	.	.	.
Total Collected			1	1	10	5	3	8

(continued on next page)

Appendix 1. (cont.)

Date	Time	Site	Insect Family or Subfamily						
			Pentatomidae	Lygaeidae	Calliphoridae	Tachinidae	Stratiomyidae	Asilidae	Chrysomelinae
July									
21	1900	WD	.	.	.	.	.	.	.
24	1900	WD	.	.	2, 1d	.	.	.	.
25	1930	WD	.	1	.	.	.	.	.
26	0900	WD	.	1	.	.	.	.	.
26	1930	WD	.	.	.	.	.	.	.
27	1915	WD	.	1	1	1	1	.	.
28	1930	WD	.	.	1d	.	.	.	.
28	2000	L	1	.	.	.	.	.	.
29	1000	L	.	.	1	.	.	.	.
29	2000	WD	.	.	.	.	.	.	.
30	2030	WD	.	.	.	.	.	.	.
31	0930	FF	.	.	.	.	.	.	.
31	2000	WD	.	.	.	.	.	.	.
August									
1	1600	L	.	.	.	.	.	.	.
3	1630	WD	.	.	.	.	.	.	.
3	1800	L	.	.	.	.	.	.	.
4	0915	WD	.	.	1	.	.	.	.
6	1630	WD	.	.	.	.	.	.	.
7	1800	DS	.	.	.	.	.	.	.
8	0930	FF	.	.	.	.	.	.	.
8	1930	WD	.	.	.	.	.	.	.
10	2000	L	.	.	.	.	.	.	.
11	1100	L	.	.	.	.	.	1	.
12	1530	WD	.	.	.	.	.	.	.
15	1000	DS	.	.	.	.	.	.	.
17	1400	L	.	.	.	.	.	.	.
Total Collected			1	3	5, 2d	1	1	1	3

(continued on next page)

Appendix 1. (cont.)

Date	Time	Site	Insect Family or Subfamily	
			Cassidinae	Cerambycidae
July				
21	1900	WD	1	.
24	1900	WD	.	.
25	1930	WD	.	.
26	0900	WD	.	1
26	1930	WD	.	.
27	1915	WD	.	.
28	1930	WD	.	.
28	2000	L	.	2
29	1000	L	.	1
29	2000	WD	.	.
30	2030	WD	.	.
31	0930	FF	.	.
31	2000	WD	.	.
August				
1	1600	L	.	.
3	1630	WD	.	.
3	1800	L	.	.
4	0915	WD	.	.
6	1630	WD	.	.
7	1800	DS	.	.
8	0930	FF	.	.
8	1930	WD	.	.
10	2000	L	.	.
11	1100	L	.	.
12	1530	WD	.	.
15	1000	DS	.	.
17	1400	L	.	.
Total Collected			1	4

Appendix 2. Insects observed, by date, with time and site

Date	Time	Site	Insect Family or Subfamily Sphingidae	Nymphalinae	Limenitinae	Danaidae	Papilionidae	Pieridae
July								
24	1700	WD	.	.	.	.	.	.
25	1400	DS	.	.	.	.	.	.
26	0900	WD	.	.	.	.	.	.
27	1600	FF	.	.	.	.	.	.
29	1000	L	.	.	.	2	.	2
30	2000	WD	2	.	.	.	.	.
31	0930	FF	.	.	.	.	.	1
August								
1	1600	L	.	.	.	.	.	.
3	1900	L	.	.	.	.	.	.
4	1000	WD	.	.	.	.	.	.
6	1630	WD	.	.	.	.	.	.
7	1800	DS	.	.	.	3	2	.
8	1000	FF	.	.	.	.	10	.
10	1800	L	.	.	.	.	.	.
11	1100	L	.	.	.	1	2	2
12	1530	WD	1	.	.	.	2	.
14	1700	FF	.	.	.	4	15	.
15	1000	DS	.	.	.	3	1	.
17	1400	L	.	.	.	.	2	.
20	0730	WD	.	.	.	2	.	.
Total Observed			3	0	0	15	34	5

(continued on next page)

Appendix 2. (cont.)

Date	Time	Site	Insect Family or Subfamily						
			Lycaen-idae	Hesper-iinae*	Pyrg-inae	Arcti-idae	Apinae	Bomb-inae	Halict-idae
July									
24	1700	WD	.	.	.	.	1	2	.
25	1400	DS	.	.	.	.	2	.	.
26	0900	WD	1	.	.	.	4	.	.
27	1600	FF	.	.	.	.	1	.	.
29	1000	L	1	.	.	.	.	4	.
30	2000	WD	.	.	.	.	.	.	.
31	0930	FF	.	.	.	.	1	.	.
August									
1	1600	L	.	.	.	.	1	6	.
3	1900	L	.	.	.	1	.	2	.
4	1000	WD	.	.	.	.	1	5	.
6	1630	WD	.	.	.	1	1	1	.
7	1800	DS	.	.	.	.	.	.	1
8	1000	FF	.	.	1	.	.	1	.
10	1800	L	1	.	.	.	.	10	.
11	1100	L	.	.	1	.	.	11	.
12	1530	WD	.	.	.	.	.	7	.
14	1700	FF	.	.	.	.	.	.	.
15	1000	DS	.	.	.	.	.	1	.
17	1400	L	2	.	.	.	.	9	.
20	0730	WD	.	.	.	.	.	5	.
Total Observed			5	0	2	2	12	64	1

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*Seven unidentified Hesperiidae were observed.

(continued on next page)

Appendix 2. (cont.)

Date	Time	Site	Insect Family or Subfamily						
			Anthophoridae	Sphecinae	Larrinae	Tiphiidae	Phymatidae	Pentatomidae	Lygaeidae
July									
24	1700	WD	.	.	.	.	1	.	.
25	1400	DS	.	.	3	.	.	.	.
26	0900	WD	.	.	1	.	2	.	1
27	1600	FF	.	.	1	.	.	.	.
29	1000	L	.	.	1	.	.	.	.
30	2000	WD	.	.	.	.	.	.	.
31	0930	FF	.	.	1	.	.	.	.
August									
1	1600	L	.	.	1	.	.	.	.
3	1900	L	.	1	.	.	.	.	.
4	1000	WD	.	.	.	4	.	.	.
6	1630	WD	.	1	.	3	.	.	.
7	1800	DS	.	.	2	.	.	.	.
8	1000	FF	.	1	1	.	.	.	.
10	1800	L	.	.	.	.	.	.	.
11	1100	L	.	2	.	.	.	.	.
12	1530	WD	.	1	.	1	.	.	.
14	1700	FF	.	.	1	.	.	.	.
15	1000	DS	.	.	.	.	.	.	.
17	1400	L	1	1	.	.	.	.	.
20	0730	WD	1	.	1	.	.	.	.
Total Observed			2	7	13	8	3	0	1

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Appendix 2. (cont.)

Date	Time	Site	Insect Family or Subfamily						
			Calliphoridae	Tachinidae	Stratiomyidae	Asilidae	Chrysomelinae	Cassidinae	Cerambycidae
July									
24	1700	WD	2	.	.	.	.	.	.
25	1400	DS	.	.	.	.	.	.	.
26	0900	WD	1	.	.	.	.	.	.
27	1600	FF	.	.	.	.	.	.	.
29	1000	L	.	.	.	.	.	.	.
30	2000	WD	.	.	.	.	.	.	1
31	0930	FF	1	.	.	.	.	.	.
August									
1	1600	L	.	.	.	.	1	.	.
3	1900	L	3	.	.	.	.	.	.
4	1000	WD	.	.	.	.	.	.	.
6	1630	WD	.	.	.	.	.	.	.
7	1800	DS	.	.	.	.	.	.	.
8	1000	FF	.	.	.	.	.	.	.
10	1800	L	.	.	.	.	.	.	.
11	1100	L	.	.	.	.	.	.	.
12	1530	WD	.	.	.	.	.	.	.
14	1700	FF	.	.	.	.	.	.	.
15	1000	DS	.	.	.	.	.	.	.
17	1400	L	.	.	.	.	.	.	.
20	0730	WD	.	.	.	.	.	.	.
Total Observed			7	0	0	0	1	0	1