

October 1982

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Available at: <http://scholar.valpo.edu/tgle/vol15/iss3/11>

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NOTES ON SHIFTING DISTRIBUTION PATTERNS AND SURVIVAL OF IMMATURE *DANAUS PLEXIPPUS* (LEPIDOPTERA: DANAIDAE) ON THE FOOD PLANT *ASCLEPIAS SYRIACA*

Susan Sullivan Borkin¹

ABSTRACT

Abundance and distribution of immature stages of the monarch butterfly, *Danaus plexippus*, on the food plant *Asclepias syriaca* were examined at a site in southeastern Wisconsin over one growing season. Estimated mortality for eggs and larvae was substantial (88%). Dispersal of larvae between individual food plants, along with egg and larval mortality factors, may result in low population density. Although the mechanism triggering larval dispersal is unknown, several alternative hypotheses are proposed for further examination.

The monarch butterfly, *Danaus plexippus* (L.), is widely distributed over North America. Considerable information has accumulated regarding its biology (e.g. Urquhart 1960; Urquhart and Urquhart 1976a, 1976b; Brower et al. 1977; Rawlins and Lederhouse, 1981), and ecological chemistry (Brower 1969, Roeske et al. 1976, Fink and Brower, 1981). Nonetheless, there are few quantified data on the population biology of the species, particularly as related to the immature stages. This paper summarizes a preliminary investigation of abundance and distribution of eggs and larvae on individual food plants and changes in these parameters through one growing season. A striking result of this study is the documentation of very low densities of eggs and larvae on food plants mitigated by the interplay of mortality and dispersal.

STUDY SITE AND METHODS

The study was conducted during 1979 at the University of Wisconsin Field Station, near Saukville, Ozaukee County, Wisconsin (43°7'N, 88°1'W). The site selected for observation was approximately 650 m² of old-field habitat with an abundance of common milkweed (*Asclepias syriaca* L.) interspersed among sweet clover (*Melilotus officinalis* L.), goldenrod (*Solidago* sp.), and various grasses. A large portion of the land surrounding the study site was mowed on 17 July 1979 for reasons unrelated to this investigation. However, the production of new *A. syriaca* growth in this mowed area during late July and early August provided an opportunity to compare exploitation of young and old milkweed plants by *D. plexippus*. The study site was therefore expanded to about 3300 m² beginning 11 August to include a portion of the mowed land.

A census of eggs and larvae was taken during daylight hours at weekly intervals beginning 2 June, the week prior to the first sightings of *D. plexippus* adults at the Field Station, through 15 September when the abundance of immatures declined dramatically. The aerial portions of milkweed plants (stem, leaves, and inflorescence) were examined for all stages of the butterfly. About 400 milkweed plants were examined on each sampling date in the unmowed portion of the study site; and an additional 250 plants on 11 August, 450 plants on 18, 25 and 31 August, and 650 plants on 8 and 15 September were examined in the mowed area.

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Numbered survey stakes were used to indicate the milkweed plants on which eggs or larvae were found. The number of eggs, number of instars of larvae, and their locations on each plant were recorded. Instar was determined on the basis of morphological differences in head capsule size, body length, and coloration. On subsequent sampling dates, the presence of any new eggs, empty or partially eaten egg shells, larvae, and areas of feeding damage were recorded. The census was maintained in this manner until no immatures were found on the plant. The stake was then removed. The height, number and color of leaves (green versus yellow), and other obvious signs of aging and herbivore damage were noted for the tagged plants.

One fourth and 25 fifth instar larvae were collected from the site and allowed to complete their development in the laboratory to estimate the incidence of tachinid fly parasitism. In addition, eggs from another locality were reared in the laboratory on selected milkweed plants from the study site to determine if the plants were capable of supporting *D. plexippus* development.

RESULTS

A total of 219 samples, representing 269 eggs and 156 first through fourth instar larvae, were monitored during the study. Some milkweeds are included more than once in the total since they were marked on more than one occasion. Larvae may also have been counted

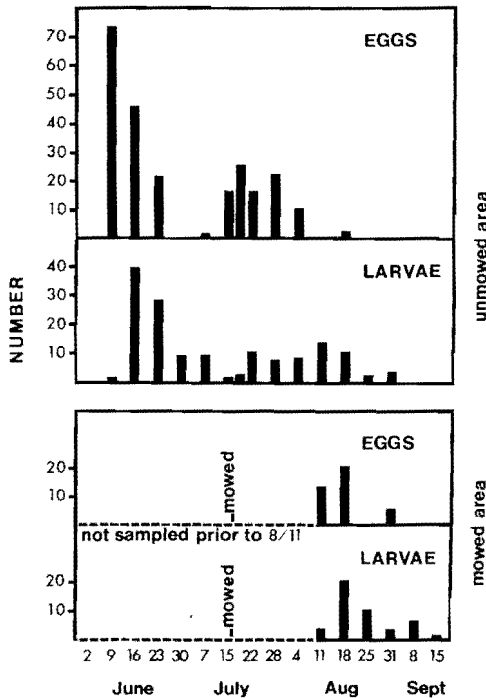


Fig. 1. Population index of *Danaus plexippus* eggs and larvae per 400 milkweed stems in the unmowed and mowed areas of the study site.

more than once as a result of dispersal occurring between sampling dates. An additional 26 larvae, all but one fifth instars, were brought into the laboratory to complete their development. The repeated searches of milkweeds failed to turn up any *D. plexippus* pupae. (The complete census history data are available on request from the author.)

Population Index

Population estimates based on the relative abundance of eggs and larvae on each sampling date are summarized in Figure 1. The data from the mowed portion of the site have been adjusted by ratio to correspond to a base figure of 400 plants searched. This enables comparison with the numbers of immatures found in the unmowed area.

The population index shows a strong peak in the number of eggs found during the second week of June corresponding to the arrival of migrating *D. plexippus* at the site. The peak in number of larvae occurring one week later was comprised mostly of first and second instars. The second peak of immatures is less pronounced than the first but extends over a longer period of time, from mid-July to late August, and represents overlapping broods. It is clearly distinguishable from the first peak based on the numbers of larvae found as first and second versus later instars. The population index also shows a shift in the distribution of immatures, from the unmowed portion of the site to the milkweeds in the mowed area, during mid- to late August. The milkweeds in the unmowed area had begun to yellow, the leaves were tough, and there was extensive herbivore damage. Those in the mowed area were green and succulent in comparison. Table 1 gives the distribution of larvae found in each area during these time periods. By September, there was a sharp decline in the *D. plexippus* population at the site, even though milkweeds were still available and temperatures were favorable for development. The first freeze in the area occurred 14 October.

Distribution of eggs and larvae

Of the total 269 eggs censused in this investigation, 152 (57%) were found distributed singly on the milkweed plants. A single egg was discovered on a blade of grass that was resting across a milkweed leaf. The remaining 116 eggs were found in combinations of up to three eggs per leaf, but no more than four eggs were found on any one plant. Approximately two-thirds of the total number of eggs were placed on the undersides of leaves. The rest were found on the dorsal leaf surfaces and a few on the stalk and flowers.

Larvae were observed feeding and resting on the food plant. Only first and second instars were observed molting. The majority of first and early second instar larvae were found concealed among the newly developing leaves. When two or more larvae occupied the same plant, they were generally found on different leaves, although on one occasion two fifth instars were seen feeding on single leaf. No observations were recorded of intraspecific aggression.

Table 1. The distribution of *Danaus plexippus* larvae according to study site area for the time periods indicated.

Site Area	Dates	No. Larvae/Instar					Totals
		1	2	3	4	5	
Unmowed	9/6-15/7	44	27	6	1	9	87 (45%)
Unmowed	19/7-15/9	23	12	5	2	13	55 (29%)
Mowed	11/8-15/9	19	14	3	1	14	51 (26%)
Totals		86 (45%)	53 (27%)	14 (7%)	4 (2%)	36 (19%)	193

Census history of eggs and larvae

Egg survivorship was assessed using two criteria. The first was the presence or absence of early instar larvae on each marked plant corresponding to the number of eggs recorded for that plant the previous week. The second was the condition of the egg shell if present, coupled with the presence or absence of typical first instar feeding damage. The pattern of feeding damage, a small circular or semi-circular area usually located close to where the egg had been, is characteristic for early instars of *D. plexippus*. Newly hatched larvae exhibit variability in the extent to which the evacuated egg shell is consumed, but the basal plate is not eaten. Partially devoured egg shells and the basal plates were therefore used as indications that eggs had survived until hatching. In most cases, the results were also supported by feeding damage. The second criterion has the advantage over the first in that it allows a measure of egg survivorship that is independent of the survival of the resulting larvae. Although egg cannibalism is known to occur under overcrowded conditions (Brower 1961), it was not found to be a significant factor in this study based on the survivorship of eggs found in combination of two or more per plant (Table 2).

First or second instar larvae were found on successive sampling dates for 81 eggs. Where no larvae were found, egg shells and feeding damage on the milkweeds indicated that survivorship was probable for an additional 74 eggs. Combined, these figures give an estimate of 58% survivorship for the eggs monitored in this study (30% when based only on the number of larvae found). Nine eggs darkened and shriveled, possibly due to some microbial pathogen or parasitism. The remaining 105 eggs were unaccounted for. Some disappeared along with portions of the milkweed plants on which they were laid as a result of the activity of insect and non-insect herbivores. A comparison of the survivorship of eggs from the first brood with eggs found in the unmowed area after June 30th indicates no significant difference for survival (χ^2 test, $P > 0.75$). Likewise, there is no significant difference in survival for eggs from the first brood compared with eggs found in the mowed area ($P > 0.1$).

One of the more intriguing results obtained in this study was that not one larva monitored completed its development on the milkweed plant where it was first recorded. Out of 155 first through fourth instars, only 17 were resighted the successive sampling date on the same plant where originally recorded and 16 were either second or early third instars at the time they were resighted. No larva was resighted on the same plant after more than one week. Table 1 illustrates a second interesting feature of the data, that is, the consistently small proportion of third and fourth instar larvae found relative to the number of fifth instars.

An example of the movement pattern for a larva which was disturbed and dropped off of its food plant is shown in Figure 2. However, I witnessed at least six examples of larvae crawling off of the food plant without disturbance. Larvae from the second instar on were observed wandering off of what appeared to be suitable milkweed plants where at least some amount of feeding had occurred. Often, a larva was found feeding on a milkweed that had

Table 2. Comparison of the survivorship of *Danaus plexippus* eggs found singly and in combinations of two or more per milkweed stem.

	Single egg per <i>Asclepias</i> stem	Two or more eggs per <i>Asclepias</i> stem
Total No. eggs	153	116
Larvae found	35 (23%)	46 (40%)
Survivorship probable	50 (33%)	24 (21%)
Egg survivorship ^a	85 (56%)	70 (61%)
Egg survivorship based only on larvae found ^b	35 (23%)	46 (40%)

^aDifference not significant (χ^2 test, $P > 0.25$).

^bDifference significant ($P < 0.01$).

been abandoned previously by another larva. I successfully reared *D. plexippus* in the laboratory from egg to imago on such plants. All of the plants tested were found to be capable of supporting development.

Of the 26 larvae that were collected and allowed to complete development in the laboratory, three (11.5%) were found to be parasitized by the tachinid, *Lespesia archippivora* (Riley). One observation was made of this tachinid in the field, attempting to oviposit on a fifth instar larva. Upon contact, the larva jerked violently from side to side, repelling the fly. The larva then dropped to the ground and crawled rapidly away from the plant. It was collected and subsequently reared through the imago. I was not able to determine whether the fly was unsuccessful in depositing an egg or some aspect of host suitability (Vinson and Iwantsch 1980) prevented development of the parasitoid.

Only one instance of predation was witnessed in the field, that of a pentatomid bug feeding on a fifth instar larva. However, other potential predators such as immature neuropterans, ants, and several species of spiders were commonly found on the milkweeds. The overall estimate of survivorship for *D. plexippus* prior to pupation is 12% in this study based on the total number of eggs and fifth instar larvae found and taking known instances of parasitism into account.

DISCUSSION

Essentially this was a descriptive study. The purpose was to investigate how *D. plexippus* exploits available larval food plants by examining abundance and distribution of immatures on the plants at one locality over a growing season. The data show that (1) only a small

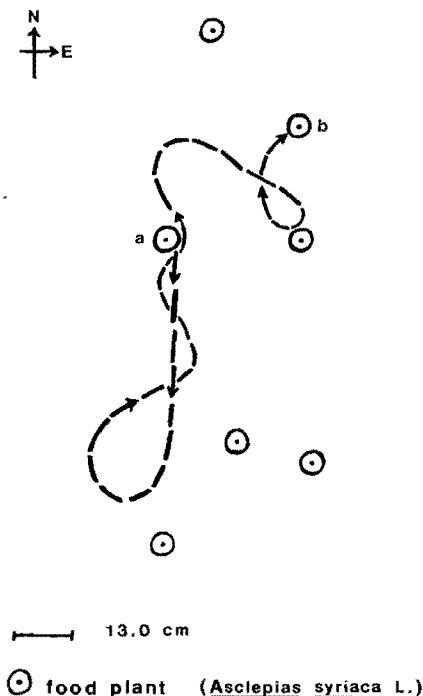


Fig. 2. Movement pattern for a larva which dropped off of its food plant.

percentage of the food plants were occupied at any given time and new growth was preferred for oviposition sites and feeding by early instar larvae, (2) eggs were killed in significant numbers throughout the growing season, and (3) the number of larvae decreased with the progression in instars, presumably as a result of mortality factors. The data also support the concept that at northern latitudes colonization of milkweeds by *D. plexippus* occurs by way of population expansion. That is, females migrate northward after overwintering and oviposit en route. The June oviposition pulse illustrated in Figure 1 represents a single brood corresponding to the arrival of migrating females at the site. The pulse beginning in mid-July represents overlapping broods, evidence of continuing northern movement by adults that developed farther south.

In addition to the population parameters just listed, it was found that individual larvae moved considerably between food plants during development even though the plants were not severely defoliated or otherwise noticeably changed. Similar results have been reported by Urquhart (1960) and Rawlins and Lederhouse (1981). The cause of this dispersal has not been determined, but it requires the expenditure of energy, and some mortality undoubtedly occurs as a direct or indirect result of the movement. For example, larvae may experience considerable difficulty in relocating a food plant, as the experiments of Dethier (1959b) and Urquhart (1960) and observations from this study (Figure 2) show. For these reasons, the proximal cues and resulting selective pressures in displacement of *D. plexippus* larvae from their food plants are of great interest.

Several alternative hypotheses can be proposed to explain the observed behavior. One is the "physiology" hypothesis, where dispersal occurs as a response to some change in the physiological condition of the larvae. For instance, a proximal cue could be related to feeding and selection pressures related to the suitability of the micro-habitat. Rawlins and Lederhouse (1981) found that feeding behavior in *D. plexippus* larvae is influenced by ambient temperature, and that active larvae tend to be feeding and in the shade. They also found that wandering off the food plant is most prevalent during midday. If this movement were for thermoregulation, one might expect the larvae to remain near the bases of the host plants and move back up the stems at a later time, as Sherman and Watt (1973) found for *Colias* larvae. Such behavior was not observed in this study nor by Rawlins and Lederhouse.

A second hypothesis is the "predator-parasitoid," where larvae disperse to escape parasitoids and other predators. Although such mortality has not been quantified, casual observations made over the past few years reveal that several species of hemipterans, spiders, lacewing larvae, and vespid wasps prey on *D. plexippus*. The aposematic coloration of *D. plexippus* larvae may serve as an adequate defense against vertebrate predators; nonetheless the results of this study indicate that mortality, likely due to invertebrate predators, is substantial. Young and Moffett (1979) found a number of arthropods kill the eggs and young larvae of *Mechantitis isthmia*, which is also considered an unpalatable species. The data support this hypothesis in part. The tachinid species found parasitizing *D. plexippus* deposits its eggs directly on the body of the host and is widespread in the United States with many lepidopterous hosts (Cole 1969) and movement off the host plant was noted for larvae that had been disturbed. However, larvae were also observed leaving the host plant without apparent cause. It seems unlikely that this hypothesis would account for the fact that not one larva completed development on its original host plant.

A third hypothesis is that of "food plant quality," where dispersal occurs as a response to some change in the physiological condition of the food plant which cannot be detected visually by researchers. The data favor this hypothesis over the preceding two. Female *D. plexippus* are highly precise in selecting a larval food plant for egg placement (Dethier 1959a, Rothschild and Schoonhoven 1977). Whether due to random selection or, more likely, to specific visual and chemical cues, some milkweeds in this study which appeared healthy (green, succulent foliage) were never utilized as oviposition sites while other milkweeds in poor condition (yellow, and with extensive herbivore damage) were found with one or more eggs. The mid-August shift in oviposition sites to the regenerated growth in the mowed area indicates a strong preference by females for young, tender plants on which to deposit their eggs, and the majority of first and second instar larvae were found on newly developing leaves. There may be a selective advantage for young larvae to feed on new growth (Coley

1980, Futuyma and Wasserman 1980, Scriber and Slansky 1981). Often food selection does not correspond with the nutritional properties of a plant (Chew 1980, Dethier 1980). Secondary plant substances may be important as attractants or feeding stimulants. Roeske et al. (1976) found the presence of secondary plant substances varies intraspecifically in *Asclepias syriaca* even among plants from the same locality. Although *D. plexippus* were successfully reared on plants that larvae had deserted, the biochemistry of the plants may have been altered when they were brought into the laboratory (J. E. Rawlins, in litt.). No measure was obtained of larval feeding preference or fitness of the resulting adults.

Any one or a combination of these proposed hypotheses can account for the shifting larval distribution patterns that were observed. Clearly, further experimental studies are required to determine the mechanism and adaptive significance, if any, of this behavior. Nonetheless, the results from this preliminary investigation suggest that in addition to egg and larval mortality factors, larval dispersal between food plants is important in the population dynamics of *D. plexippus*.

ACKNOWLEDGMENTS

This study was conducted as part of a Master's degree program. I gratefully acknowledge A. M. Young for guidance throughout the project. I also thank J. E. Rawlins for reviewing the manuscript, M. Ficken, University of Wisconsin-Milwaukee, for suggestions and use of the Field Station facilities, C. W. Sabrosky, USDA Systematic Entomology Laboratory, for the tachinid determination, and A. Borkin for encouragement.

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