J. Zool., Lond. (1982) **198**, 103–116

Dynamics of oviposition in *Danaus plexippus* (Insecta: Lepidoptera) on milkweed, *Asclepias* spp

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(*Accepted 10 November 1981*)

(With 5 figures in the text)

Where a butterfly chooses to lay an egg will influence the subsequent survival of her offspring. In this paper we report on the effect of a number of variables which influence the choice of oviposition site in *Danaus plexippus* L. Experiments were conducted under both flight cage and field conditions. The field observations consisted of recording the within and between plant egg dispersions across different patch sizes. Laboratory experiments looked at egg laying preferences as affected by plant species, age and condition. Butterflies were selective in their choice of oviposition site. Eggs were laid singly on the underside of medium sized leaves towards the top of a plant. More eggs were laid per plant on single isolated plants than on plants within a patch. The number of eggs per plant increases with plant height but decreases with plant age. Females preferred young plants or plants with fresh regrowth of leaves. These characteristics could override species preferences which were, in decreasing order, *Asclepias curassavica*, *A. fruticosa* and *A. physocarpa*. Species preferences varied between butterflies and with female age. Neither the presence of eggs nor larvae on a plant deterred oviposition. These results are compared with previous observations of egg laying in this species.

Contents

Introduction

Where an adult female butterfly chooses to deposit her eggs will influence the survival of her offspring and, consequently, her overall fitness. An egg present on a plant represents a record of the outcome of the various choices a butterfly makes in selecting among alternative potential oviposition sites and the factors that influence these choices. A knowledge of

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the dispersion of a butterfly's eggs does not, however, enable any inference about the behavioural patterns which generated the pattern (see e.g. Harcourt, 1961; Kobayashi, 1966; Monro, 1967; Iwao & Kuno, 1968, 1971). The pattern observed can only be understood if studies on egg-laying responses are linked to detailed investigations of the searching behaviour of the animals concerned. There have been few attempts to combine population and individual behaviour studies in this fashion (but see Jones, 1977; Ives, 1978; Jones & Ives, 1979).

In this paper we describe the egg laying responses of *Danaus plexippus* to various species of *Asclepias*. In particular we look at the effects of plant size, quality, species and spatial dispersion on the number of eggs laid.

Ives (1978) identifies three spatial scales which, potentially, may influence egg laying. These are (i) differences among leaves on the same plant—Jones & Ives (1979) suggest that leaf choice may influence survival of early instars; (ii) differences among plants within the same patch – a patch can be defined as a group of plants in which each plant is less than twice a butterfly's perceptive distance from its nearest neighbour (see Gilbert, Gutierrez *et al.*, 1976; Ives, 1978) and factors such as age, species and size of plant which have been shown to influence development and survival of eggs and larvae (Pimentel, 1961; Hovanitz & Chang, 1962; Jones & Ives, 1979); and (iii) differences among patches of plants—patch size has been shown to influence the number of eggs a plant receives, as has relative plant position (Cromartie, 1975; Jones, 1977) and this also influences larval survival and levels of parasitism (Zalucki, 1981*b*; Zalucki & Kitching, in press).

Materials and methods

Field-plot experiments were performed on Griffith University Campus (lat. 27°30'S; long. 153°E). Laboratory experiments were done in a large flight cage measuring 5 × 4·85 × 2 m, located on the roof of the Environmental Studies building, Griffith University. The flight cage was divided using mesh partitions into four equally sized compartments so that four separate experiments could be run simultaneously. Butterflies used in the flight cage were first generation laboratory reared specimens. Butterflies in the field work were wild ones which encountered the experimental plots in the course of their natural patterns of movement.

All plants used in this work were grown in pots from seeds collected in the field (around Beenleigh, lat. 27°43'S; long. 153°12'E). Plants were kept in a glasshouse until needed. Glasshouse temperature was set to 25° ± 4°C and daylength increased during winter months by using supplementary lighting. The main plant species used were three species of *Asclepias*: *A. curassavica* L., *A. fruticosa* L. and *A. physocarpa* (E. May) Schlecht. The latter two species have been placed into the genus *Gomphocarpus* by some authors (e.g. Smithers, 1973; Dixon *et al.*, 1978) however Everist (1974) retains them in the genus *Ascelpias* and we follow his nomenclature. Experimental design was dictated by availability of plants and butterflies and hence some comparisons were not possible.

Field experiments

Sixty-four *A. fruticosa* plants were placed out in pots at the University site in two locations. Both were on cleared plots of land surrounded by secondary regrowth of sclerophyll forest. Similar treatments were established at each location to investigate the effects of patch size (Table I(a)). All plants were spaced 1 m apart, except for the single plants which were 10 m or more from their nearest neighbour plants. All plants were searched every two days, from the 28.9.77 to 12.10.77, for *D. plexippus* eggs. For each plant the following information was recorded on each occasion: (a) plant height, (b) length of leaves with eggs, (c) the height of the egg-bearing leaves above ground, (d) the number of eggs on the leaf, (e) which surface the egg was laid upon (upper leaf, lower leaf or stem) and (f) total number of eggs on the plant.

This experiment yielded information on the effect of patch size on eggs laid per plant and where on a plant eggs are laid in terms of leaf size and position. The larger patch size also provided information on within-patch dispersion of eggs. To gain a clearer indication of the latter, much larger patches of 90 (18.5.79–7.6.79) and 110 plants (26.6.79–1.7.79) were established at Tanah Merah, and the number of eggs occurring on each plant recorded regularly. One count of eggs per plant was made within a large natural milkweed patch and on some isolated single plants. This count served as a check on the effects of patch size obtained using experimental patches.

Laboratory experiments

On three occasions different combinations of plant species and plants of varying type (old, damaged) were set up in the flight cage and newly emerged male and female butterflies released into the cages (see Table I(b)). The lack of symmetry in the various experiments (Table I(b)) reflects the differing availability of suitable plants. *Experiment 1* looked for any changes in *D. plexippus* egg laying prefer-

TABLE I

(a) *Patch size treatments at each campus site*

2 × single plants > 10 m from nearest neighbour
1 × 2 plants side by side 1 m apart
1 × 4 plants in a square 1 m on a side
1 × 8 plants in a ring 1 m between plants
1 × 16 plants in a lattice square 1 m between plants

(b) *Plant treatments in each flight cage compartment for egg laying preference experiments (see Text)*

Experiment	Compartment 1	2	3	4	♀/compartment	Duration (days)
I 4/11/78–16/12/78	3/P/M67 3/F/M/113 2/C/O/59	3/P/M/68 3/F/M/79 2/C/O/124	3/P/M/60 3/F/M/100 2/C/O/87	3/P/M/71 3/F/M/90 2/C/O/98	5	42
II 2/2/79–19/2/80	2/P/M/50 2/F/M/41 2/C/M/36 1/A/M/100 1/CG/O/50	2/P/O/950 2/P/M/240 3/P/Y/69	2/F/O/574 3/F/M/72 1/F/Y/715	2/C/O/336 1/C/M/23 3/C/Y/32	3	17
III 29/3/79–9/5/79	1/P/R/43 1/F/R/37 1/C/R/30 1/P/M/33 1/F/M/47 1/C/M/25	2/P/M/90 2/F/R/66 2/C/M/54	2/P/R/72 2/F/M/78 2/C/M/45	2/P/M/78 2/F/M/85 2/C/R/39	5	41

Nomenclature: No. plants/species/age or condition/total height at beginning (cm) P, *A. physocarpa*; F, *A. fruticosa*; C, *A. curassavica*; A, *Araujia* spp; CG, *Cryptostegia* spp.; O, old, > 1 year; M, medium, 3 months < x < 1 year; Y, young, < 3 months; R, regenerating.

ences over the adults' life span. The butterflies were offered a choice of the three available species of *Asclepias* (Table I(b)). In this, as in all the experiments, the plants were moved to new positions in the flight cage compartment after each egg-count to obviate any effects of position. Eggs were counted and removed daily. *Experiment 2* looked at the effects of plant height and age on numbers of eggs laid per plant. One compartment repeated the treatment used in *Experiment 1*, with the added choice of an *Araujia hortorum* Fournier (moth plant) and a *Cryptostegia grandiflora* R.Br. (rubber vine), both Asclepiadaceae and therefore potential host plants. The remaining three compartments contained only plants of each of the three *Asclepias* spp. (Table I(b)).

Eggs were counted and removed daily from 2.2.79 until 12.2.79 when the eggs laid on that day (and on the 13th) were circled and left on the plants. This provided an indication of the effects of eggs left on the plant on subsequent egg laying. The eggs laid on the 12th and 13th were allowed to hatch and the larvae to feed on the plants on the 16.2.79 and 17.2.79. This treatment looked for any response by females to plants showing signs of larval feeding activity.

Experiment 3 compared plants with re-growth (regenerating) versus plants without such growth. Plants classified as "regenerating" had been first defoliated by *D. plexippus* larvae, and placed into the flight cage when new leaves started to appear (see Table I(b) for treatment). Eggs were counted and removed daily.

Results

Field experiments

Location of eggs

D. plexippus lays eggs singly, rarely is more than one egg found on a leaf. Of the 1644 eggs laid in the field experiment, the vast majority (88%) were laid singly, 8·6% (142) were laid in pairs, 3·3% (54) in threes and 0·5% (8) were laid in two groups of four. Eggs were also deposited predominantly on the underside of leaves (96·5%) rarely on the upper surface (3·2%) or stem of a plant (0·3%). These results agree with observations reported in Urquhart (1960).

Within plant egg dispersion

Plants were not laid in a uniform manner over a plant ($\chi^2_9 = 52{\cdot}14$, $P < 0{\cdot}005$, Fig. 1). The leaves on which eggs were laid were located towards the top of the plant. Of the 117 eggs for which leaf heights above ground, relative to plant height, were measured, 75% were laid on the top half of the plant (Fig. 1). Most eggs were laid at around 80–90% of the plant's height from the ground. Consequently, eggs were not concentrated on the smallest leaf size class, which occur around the apex (top 10%) of the plant (Fig. 2). Very few were laid on the smallest (< 50 mm in length) and largest (> 140 mm) leaves. Most (87%) were laid on the middle-sized leaves (50–140 mm; Fig. 2).

Effect of plant height

The numbers of eggs laid on plants which were in a group size of 8 (site 4 and 5, Table I(a), all plants were edge plants) were regressed against plant heights. Tall plants receive significantly more eggs than smaller plants $F^1_{54} = 3{\cdot}331$. $P < 0{\cdot}10$; $F^1_{61} = 13{\cdot}84$, $P < 0{\cdot}0005$) although the regression coefficient is small in each case (0·2 and 0·17 respectively). This implies that there is about one additional egg for every 5 cm increase in height. These regressions are somewhat misleading, as the number of eggs laid on a plant does not increase continually with height, but depends also on the age of the plant (Expt. 2).

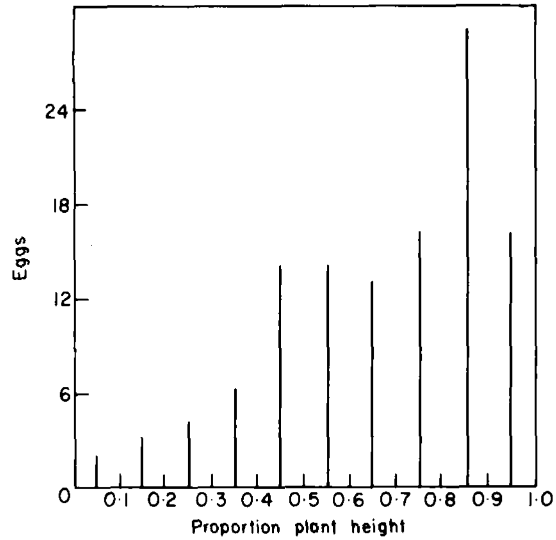

FIG. 1. Eggs laid plotted against the proportion of plant height above the ground at which they were laid.

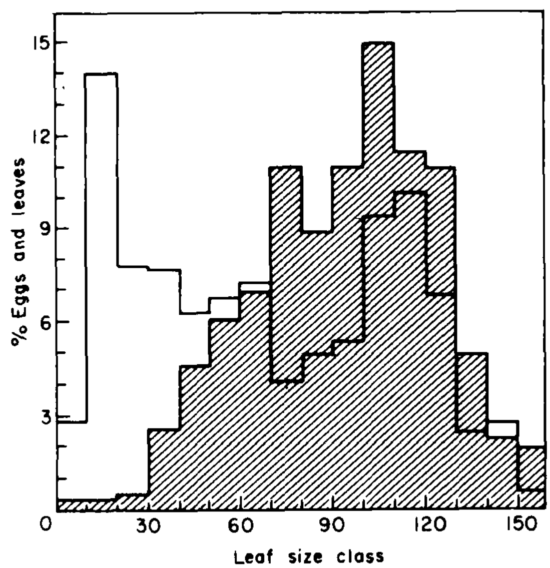

FIG. 2. Percentage leaves and eggs (cross-hatched) plotted against leaf size class in mm.

Effects of patch size

To analyse for the effects of patch size on the number of eggs laid per plant an analysis of variance was performed, the variable analysed being eggs counted on each sampling occasion. These counts were designated by site, patch size and sample date. There were significant interactions between site and time, and size and time. To isolate the effects of the size of a patch, the egg counts on each sample date were analysed separately by site, using a one-way analysis of variance, the treatments being determined by patch size. This indicated that patch size has a significant effect on the number of eggs laid per plant on most sampling occasions. On those sampling times when the effect of patch size was significant, the trend was for a decrease of egg/plant as patch size increased. Taken over the whole period of the experiment, the results are variable although there is a weak trend in the same direction as was observed on most separate sampling occasions (Fig. 3(a)). Patch sizes varied in the experiments by a factor of 16. In the field, patches ranged from single plants to large areas 2–300 m in diameter (Zalucki, Chandica *et al.,* 1981). The single field count from 20 single plants and 20 plants from a large (20 m diameter) patch shows the effect of patch size more clearly (Fig. 3(a)).

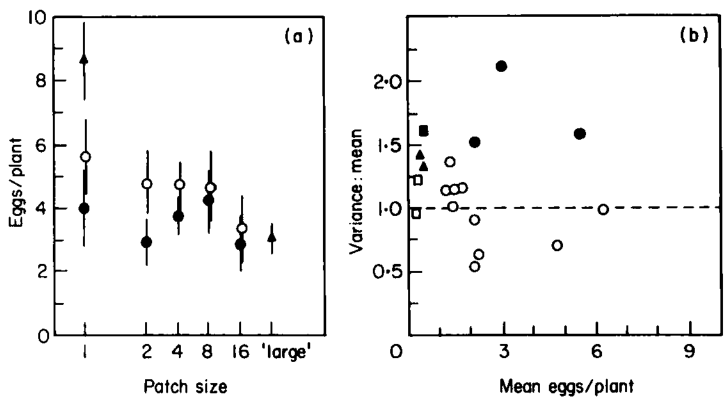

FIG. 3. (a) Eggs laid per plant plotted against patch size (±S.E.) for campus site 1 (○), site 2 (●) and field collection (▲). (b) Variance/mean ratio of eggs per plant plotted against the average number of eggs/plant for patch sizes of 16 (○), 90 (□) and 110 plants (△). Solid symbols indicate points significantly different from 1 (χ^2 test) and indicate clumping. Open symbols indicate points *not* significantly different from 1 and indicate a random dispersion.

TABLE II
Dispersion of eggs within patches

Patch size	16*		90			110		
Plant classification**	E	I	E	I	W	E	I	W
Number of plants	12	4	34	26	30	38	30	42
Total eggs	587	215	51	26	10	48	23	22
Sample times	8		3			2		
χ^2***	1·25		22·35			13·1		
Eggs/plant/sample time	6·1	6·7	0·5	0·3	0·1	0·6	0·4	0·3

*Two university sites combined: **E, edge or outer ring of plants; I, inner or next ring of plants; W, remaining plants at the centre of the patch. ***χ^2 test for uniformity, $P < 0·005$.

Within patch dispersion

Eggs were not evenly distributed within a patch (Table II). Eggs usually show a clumped dispersion pattern (Variance/mean > 1; χ^2 test Fig. 3(b)). Female *D. plexippus* appear to prefer to lay eggs on some plants more than others. More eggs were laid on plants at the edge of patches than on plants within the patch (Table II), although the edge effect is stronger the larger the patch.

Laboratory experiments

Experiment 1

Effects of time and differences between butterflies. A female's choice of plant species on which to oviposit varied greatly both among butterflies and with the age of the butterfly and preferences changed from day to day. Pooling the results over time (42 days) in three out of four compartments, *A. fruticosa* plants received more eggs than did *A. physocarpa* (in one compartment this preference was reversed) and in all cases, old *A. curassavica* plants received least eggs (Ratios *A. f.* : *A. p.* : *A. c.* were; 0·40 : 0·36 : 0·24 (5084 eggs); 0·50 : 0·40 : 0·10 (4109 eggs); 0·42 : 0·33 : 0·25 (3542 eggs); 0·32 : 0·50 : 0·18 (4468 egss)).

Experiment 2

(a) *Species preferences.* Plants used in this experiment were of a similar age and height and had similar shape characteristics. As in Experiment 1 the proportion of each day's eggs laid on the different species was again highly variable from day to day. The total number of eggs laid on each of the five species offered was not distributed uniformly.

Of the 824 eggs laid over 17 days, none were deposited on the rubber vine, *Cryptostegia grandiflora* and only 14 on *Araujia hortorum.* The three other plant species may be ranked in terms of oviposition preferences, *viz.* (1) *A. curassavica* (353 eggs); (2) *A. fruticosa* (252 eggs); (3) *A. physocarpa* (210 eggs). An indication of the variability of oviposition preferences can be seen if we look at egg counts after six days, *viz.*: (1) *A. curassavica* (127 eggs); (2) *A. fruticosa* (111 eggs); (3) *A. physocarpa* (74 eggs). Although the order of preference is the same, *A. curassavica* was not as strongly preferred as before.

TABLE III

Total eggs laid on plants in Expt II, cages 2, 3 and 4

				Plant designation				
Cage 2	Old (fl)	Old (fl)	Med	Med	Young	Young	Young	*A. physocarpa*
Ht (cm)*	770	180	186	54	27	26	16	
Total eggs	246	135	314	241	73	135	82	
E/Ht	0·32	0·75	1·69	4·46	2·70	5·23	5·13	
Cage 3	Old (fl)	Old (fl)	Med	Med	Med	Young		*A. fruticosa*
Ht (cm)*	369	205	24	24	24	15		
Total eggs	171	137	85	66	81	48		
E/Ht	0·46	0·67	3·54	2·75	3·38	3·20		
Cage 4	Old (fl)	Old (fl)	Med	Med	Young	Young		*A. curassavica*
Ht (cm)*	254	82	23	14	9	9		
Total eggs	199	42	281	179	98	105		
E/Ht	0·78	0·51	12·22	12·79	10·89	11·67		

*Total plant length (height and branches); fl, flowering; Ht, height in cm; E, eggs.

(b) *Plant age and height.* Field results indicated a significant effect of plant height on number of eggs laid, although plant age is also important (see field results and Table III). In the laboratory, old large plants (in flower, and with pods) received fewer eggs per unit plant height than did younger smaller plants.

(c) *Effect of the presence of eggs on plants.* Eggs left on the plant had no effect on subsequent egg laying. The regression of eggs subsequently laid versus eggs left on the plant was $Y = 2{\cdot}37 - 0{\cdot}92\ X\ (F^1_{23} = 63{\cdot}55,\ P < 0{\cdot}001$, Fig. 4). The slope and intercept did not differ significantly from 1 and 0 respectively ($t = 0{\cdot}7342$ and $t = 0{\cdot}4255$ respectively; $P < 0{\cdot}01$ in both cases). The regression of subsequent eggs versus two days of accumulated eggs was $Y = 0{\cdot}91 + 0{\cdot}46\ X\ (F^1_{17} = 103{\cdot}6,\ P < 0{\cdot}001$, Fig. 4). The slope and intercept did not differ from 0·5 and 0 ($t = 0{\cdot}9243$ and $t = 0{\cdot}2135$ respectively; $P < 0{\cdot}01$ in both cases). Doubling the number of eggs per plant has no effect on the number of eggs laid subsequently (slope $= 0{\cdot}5$), that is the number of eggs laid on each plant was about the same for the three days of the treatment. The presence of eggs has no effect on subsequent egg laying.

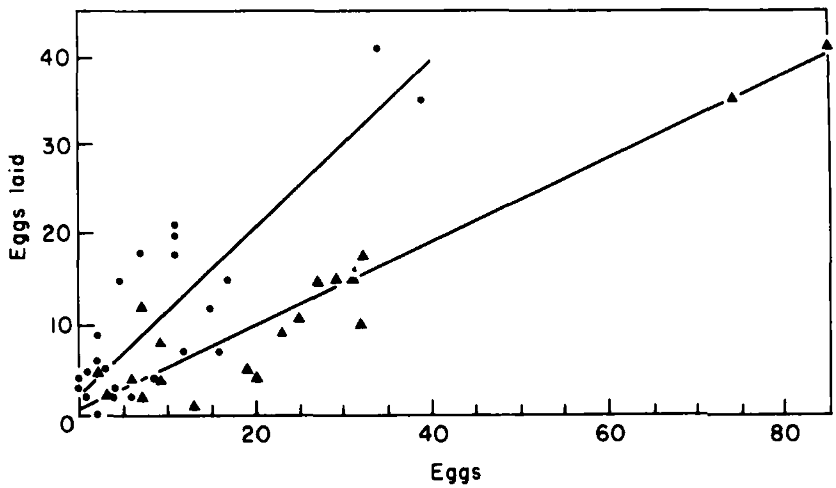

FIG. 4. Scatter plot of eggs laid/plant against eggs remaining on plant after one day's egg-laying (●) and after two days (▲). See text for regression equations.

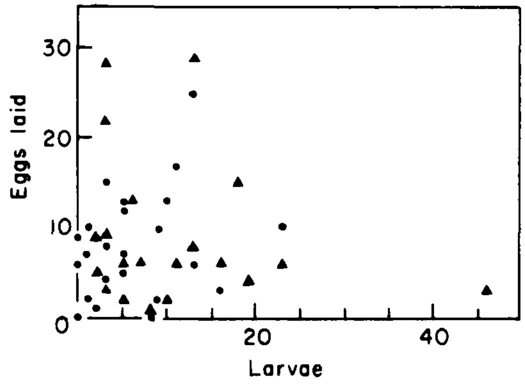

FIG. 5. Scatter plot of eggs laid/plant against larvae numbers/plant after one day (●) and after two days (▲).

(d) *Effect of the presence of larvae on plants.* Larvae, in densities ranging from 0 to 46 per plant, had no effect on the subsequent number of eggs laid, either on day one ($F^1_{23} = 2{\cdot}371$, $P > 0{\cdot}10$), day two ($F^1_{23} = 0{\cdot}8303$, $P > 0{\cdot}10$) or for the two days combined ($F^1_{47} = 0{\cdot}0358$, $P > 0{\cdot}10$; see Fig. 5). Although the regressions are not significant, the trend in the regression coefficients suggests that the presence of larvae may act as a mild deterrent to oviposition (slope = 0·31 on day 1, −0·14 on day 2 and −0·02 overall).

TABLE IV

Total eggs laid on plants in Expt 3

Species Treatment**	N	Ht	Eggs	E/Ht	N*	Ht	Eggs	E/Ht
	Cage 1				Cage 2			
A.C.	1	25	60	2·4	2	54	484	8·96
A.C/R	1	30	282	9·4				
A.P.	1	33	120	3·6	2	90	528	5·87
A.P/R	1	43	241	5·6				
A.F.	1	47	56	1·2				
A.F/R	1	37	207	5·6	2	66	657	9·95
Species Treatment**	N	Ht	Eggs	E/Ht	N	Ht	Eggs	E/Ht
	Cage 3				Cage 4			
A.C.	2	45	369	8·20				
A.C/R					2	39	332	8·51
A.P.					2	78	264	3·38
A.P/R	2	62	238	3·84				
A.F.	2	78	282	3·62	2	85	206	2·42
A.F/R								

*N, number of plants in treatment; Ht, height in cm; E, eggs.

**A.C., *A. curassavica*; A.F., *A. fruticosa*; A.P., *A. physocarpa*; /R, with regrowth.

Experiment 3

Effects of plant condition. Females prefer to lay on plants with regenerating leaves as opposed to those without such leaves (Table IV). This was the case across all three species except in compartment 3. Here *A. curassavica* received more eggs/unit plant length than *A. physocarpa* with regenerating leaves. Basically *A. curassavica* is a preferred oviposition plant (*Experiment 2(a)* above) although plant age (*Experiment 1* above) and/or the presence of fresh growth (Table IV) may override this preference.

Discussion

Danaus plexippus females exercised considerable selection in their choice of sites on which to lay eggs. Fewer eggs were laid/plant on plants in large patches compared with single plants; and on plants at the edge of the patch compared with plants within the patch centre. In these respects *D. plexippus* is very similar to *Pieris rapae* (see Cromartie, 1975). Jones (1977) suggested that such an effect—the greater frequency of encounter with isolated plants may arise if a searching female locates a patch by perceiving its edge, then isolated plants will present more edge than plants within a dense clump. Hence edge plants will be encountered more frequently and receive a greater number of eggs. The spreading and spacing of eggs by *D. plexippus* among many plants and patches of plants would "spread the risk" (*sensu* Reddingius & den Boer, 1970) of any one female's progeny going extinct among many different microhabitats.

The simplest hypothesis one can entertain on host plant selection by ovipositing females is that only those sites (plants) are chosen which will provide the most suitable environment for immature survival and development (Gilbert & Singer, 1975; Jones & Ives, 1979; Wicklund, 1977). Views vary as to which factors are most important in terms of the nature of the plant, some advocating nutritional factors (Fennah, 1953; Kennedy, 1969; Jones & Ives, 1979) and others, secondary plant substances (Dethier, 1970; Fraenkel, 1969). However, the choice made by a female is not necessarily the one with the best survival potential (Raucher, 1979) or the choice a larva would make (Singer, 1971).

Danaus plexippus lays eggs almost exclusively on plants of the family Asclepiadaceae, and is recorded from a wide range of milkweeds in North America (Urquhart, 1960; Brower, 1961) and a smaller range of imported milkweeds in Australia (Common & Waterhouse, 1972; Smithers, 1973; Koch *et al.*, 1977).

There is some controversy in the literature as to the preferences for different plant species in *D. plexippus*. Brower (1962) reported that females (in the field) laid more eggs on the more toxic *A. humistrata* than on the less toxic *A. tuberosa* in the same area. Brower (1969) using this and other pieces of information suggested that female *D. plexippus* cue in on secondary plant substances, particularly cardiac glycosides and oviposit preferentially on those plants containing large amounts of these compounds.

Dixon *et al.* (1978), on the other hand, reported that butterflies consistently selected (except for one aberrant case) plants with the lowest concentration of cardiac glycosides of those plants offered. Their preference in descending order was *A. (Gomphocarpus) fruticosa* and *Calotropis gigantea* which reflects cardiac glycoside content in increasing order.

Our results based on cumulative egg counts over long periods of time indicate that for plants of similar age, height, shape and condition, *D. plexippus* preferred *A. curassavica* > *A. fruticosa* > *A. physocarpa* > *Araujia* sp. The first three species could be arranged in the following order of decreasing cardiac glycoside concentration: *A. curassavica* > *A. physocarpa* > *A. fruticosa* (Table V). Unfortunately the plants used for cardiac glycoside determination were not the same ones as those used in the preference tests. There is a suggestion that *D. plexippus* laid preferentially on plants with a higher cardiac glycoside content. However given the range of glycoside concentrations recorded both within and between plant species (Table V) this result is inconclusive. There is no reason why animals should select plants with either high or low concentration of the relevant secondary plant compound. Just as plausible is the existence of optimal concentrations of compounds. This optimum may vary from butterfly to butterfly and plant to plant. Clearcut relationships between plant species and oviposition may therefore be difficult to obtain.

Plant secondary compounds are not the only criteria used by females to select a host plant and/or leaf on which to oviposit. Age, height and condition are also important variables, and the results somewhat more clear cut. Plants with new growth are preferred to those without and plants with wilted leaves are avoided (see also Urquhart, 1960; Dixon *et al.*, 1978).

TABLE V

Total cardiac glycoside concentration (mg/g of material) in three species of milkweed

A. curassavica	*A. fruticosa*	*A. physocarpa*
3·99[a][c]	0·84[f]	0·06[e]
0·56[b][d]		
0·58[e]	0·63[b]	
	3·3[c]	
	0·04[e]	

[a]Roeske *et al.* (1976), average for upper, middle and lower leaves.

[b]Rothschild *et al.* (1975) various plant fractions.

[c]Seiber *et al.* (1980), leaves of *A. curassavica* and "*Gomphocarpus* spp".

[d]Benson & Seiber (1978) sum of calotropin and calactin concentrations.

[e]Mitchell (1978), leaves.

[f]Watson & Wright (1956), leaves.

In the field old (large) and very young (small) leaves are avoided, the butterflies preferring to lay on the larger middle-sized leaves on the top 20% of the plant. Neither Urquhart (1960) or Dixon *et al.* (1978) measured the leaf sizes selected for oviposition, but used terms such as "small" or "tiny" so no precise comparison with the present work is possible. Eggs laid per plant increase with plant height (size), if the plants are not too old. Old plants are avoided and age can override species preferences (see *Experiment 1* in which old *A. curassavica* were avoided). Chew (1975) points out that species which lay eggs singly and visit many different host plants may be slow to evolve consistent species preferences. However there would be strong intra-host selection, since a poor plant for larval development, in terms of plant condition, would be much the same across plant species (Jones & Ives, 1977).

The importance of the effect of plant condition on larval survival and development was not investigated in this study although many authors have suggested recently that the growth and performance of populations of herbivorous insects is closely tied to plant nutritative qualities, particularly the amount and availability of nitrogen (White, 1974; Barbosa & Greenblatt, 1979; Lewis, 1979). This may account for the selection of plants with fresh growth as opposed to old, and the plant's top growing leaves as opposed to old yellowing leaves at the base. Although Schroeder (1976) showed that instar V *D. plexippus* were not limited either by the quantity or availability of nitrogen in their food, this does not rule out the importance of nitrogen (and other aspects of food quality) to early instars.

Danaus plexippus females did not avoid plants already bearing eggs or small numbers of early instar larvae. This is contrary to the findings of Urquhart (1960) and Dixon *et al.* (1978) who report that the presence of eggs and larvae deterred oviposition. It must be noted that Dixon *et al.* (1978) used extremely high egg densities—between 145–775 eggs were left on first year plants, whereas we used between 1–85 eggs. We have never observed densities such as those used by Dixon *et al.* (1978) in Australia: in the field our maximum figure was one record of 21 eggs on an isolated single plant. The larval densities used by Dixon *et al.* (1978) were not reported. Urquhart (1960) reported that monarchs avoided seedlings bearing one egg. How these observations were made and what sample sizes are involved is not clear from his comments. Certainly monarchs in Australia do not avoid plants bearing eggs (Zalucki, 1981*a*).

The non-avoidance of plants bearing eggs and larvae may seem maladaptive, particularly as *D. plexippus* larvae are potentially cannibalistic. However, due to the low survival of eggs and early instars (Zalucki & Kitching, In press), the loss of eggs due to conspecifics in the field would be rare. Furthermore, *D. plexippus* spreads its eggs around, rarely overloading plants.

Summary

The egg laying responses of female *Danaus plexippus* to *Asclepias* spp. in terms of plant size, quality, species, the presence of eggs and larvae and the spatial dispersion of plants was assessed under flight cage and field conditions. Females exercise considerable selection when "choosing" an oviposition site. The egg laying pattern may be summarized as follows:

(a) eggs were laid singly on the underside of leaves;

(b) within a plant, middle-sized leaves (50–140 mm) towards the top of a plant were preferred;

(c) more eggs were laid per plant on single isolated plants than on plants within a group (or patch);

(d) within a patch more eggs were laid on edge than on non-edge plants;

(e) the number of eggs per plant increases with plant height but decreases with plant age;

(f) female oviposition preferences in decreasing order were *Asclepias curassavica, A. fruticosa, A. physocarpa*;

(g) species preferences could be obviated by plant age and condition, young plants and plants with regrowth being preferred;

(h) species preferences varied among butterflies and with butterfly age;

(i) the presence of eggs and larvae did not influence oviposition.

The authors are indebted to all those unpaid assistants who helped with egg counts and to D. W. Connell for making research facilities available to us. One of us (MPZ) was supported by a C.P.R.A. Scholarship.

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