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SELECTIVE OVIPOSITION BY MONARCH BUTTERFLIES (*DANAUS PLEXIPPUS* L.) IN A MIXED STAND OF *ASCLEPIAS CURASSAVICA* L. AND *A. INCARNATA* L. IN SOUTH FLORIDA

STEPHEN B. MALCOLM AND LINCOLN P. BROWER
Department of Zoology, University of Florida,
Gainesville, Florida 32611

ABSTRACT. Host plant selection by ovipositing monarch butterflies occurred in a mixed stand of the milkweeds *Asclepias curassavica* and *A. incarnata* in a south Florida pasture. Three times more immature monarchs were found on *A. curassavica* than on *A. incarnata*. When these numbers were balanced for biomass differences between the two plant species, there were 5.7 times the number of monarch immatures/dry leaf mass/100 m^2 on *A. curassavica* than on *A. incarnata*. Since *A. curassavica* had 36 times more cardenolide than *A. incarnata*, we suggest that the basis for selective oviposition by monarchs is to provide an effective cardenolide-based defense for their offspring.

Only 27 of the 108 North American species of the milkweed genus *Asclepias* (Woodson 1954) have been recorded as larval food plants of monarch butterflies, *Danaus plexippus* L. (Table 1). This restricted use of host species may reflect host availability, or active host selection. If, as Dixon et al. (1978) suggest, ovipositing monarchs do not discriminate between milkweed species on the basis of their cardenolide content, the criteria that determine patterns of resource use are likely to be based on the abundance, temporal and spatial distribution, and habitat diversity of different *Asclepias* species. On the other hand, Brower (1961) found that ovipositing female monarchs in south central Florida selected *A. humistrata* rather than nearby *A. tuberosa* plants. Such host selection may well be influenced by variations in leaf biomass and morphology, qualitative and quantitative chemical defenses, and nutritive value, between *Asclepias* species, as Price and Willson (1976) have suggested for another milkweed feeding specialist.

Recent observations near Gainesville, north Florida, in spring 1983 and 1984, indicate that monarchs do not lay eggs on the common milkweeds *A. tuberosa* and *A. verticillata* and rarely lay eggs on two less common species, *A. amplexicaulis* and *A. tomentosa*. These four species have low cardenolide concentrations and are medium-sized to small plants (Table 2; Roeske et al. 1976). Two other common milkweed species, *A. humistrata* and *A. viridis*, are heavily exploited by ovipositing females from early April to June (Malcolm et al. 1987). Interestingly, these two milkweeds contain the highest concentrations of cardenolides and have the largest leaf biomass of the available species in north Florida (Table 2). Since monarchs are well known for their ability to store milkweed-derived cardenolides as a defense against

TABLE 1. North American *Asclepias* species serving as hosts of monarch butterfly larvae in nature.

Asclepias species	Location	Reference
humistrata	Florida	Brower (1961, 1962), Nishio (1980), Cohen and Brower (1982), Nishio et al. (1983), Malcolm et al. (1987)
	Georgia	Nishio (1980), Nishio et al. (1983)
syriaca	Illinois	Price and Willson (1979)
	Michigan	Wilbur (1976), Malcolm and Cockrell, unpubl.
	New York	Rawlins and Lederhouse (1981), Malcolm and Cockrell, unpubl.
	Pennsylvania	Schroeder (1976), Malcolm and Cockrell, unpubl.
	Ontario	Beall (1948), Urquhart (1960), Malcolm and Cockrell, unpubl.
	Wisconsin	Barker and Herman (1976), Borkin (1982), Malcolm, Cockrell, Brower, and Brower, unpubl.
	North Dakota	Malcolm and Cockrell, unpubl.
	Minnesota	Malcolm and Cockrell, unpubl.
	Vermont	Malcolm and Cockrell, unpubl.
	Connecticut	Malcolm and Cockrell, unpubl.
	New Jersey	Malcolm and Cockrell, unpubl.
	Maryland	Malcolm and Cockrell, unpubl.
	Virginia	Malcolm and Cockrell, unpubl.
	Missouri	Malcolm and Cockrell, unpubl.
	Kansas	Malcolm and Cockrell, unpubl.
	Nebraska	Malcolm and Cockrell, unpubl.
	Iowa	Malcolm and Cockrell, unpubl.
	Ohio	Brower and Brower, unpubl.
viridis	Florida	Brower, Cockrell, and Malcolm, unpubl.
	Louisiana	Lynch and Martin, unpubl.
	Texas	Malcolm and Cockrell, unpubl.
	Arkansas	Malcolm and Cockrell, unpubl.
	Oklahoma	Malcolm and Cockrell, unpubl.
	Missouri	Malcolm and Cockrell, unpubl.
	Kansas	Malcolm and Cockrell, unpubl.
asperula	Texas	Malcolm, Cockrell, Lynch, and Martin, unpubl.
tomentosa	Florida	Brower, Cockrell, and Malcolm, unpubl.
obovata?	Louisiana	Malcolm and Cockrell, unpubl.
	Texas	Malcolm and Cockrell, unpubl.
curassavica	Florida	Brower (1961), this paper
incarnata	Florida	Brower (1961), this paper
	Kansas	Malcolm and Cockrell, unpubl.
	Wisconsin	Brower and Brower, unpubl.
longifolia	Louisiana	Riley, Lynch, and Martin, unpubl.
hirtella	Arkansas	Malcolm and Cockrell, unpubl.
	Missouri	Malcolm and Cockrell, unpubl.
viridiflora	Michigan	Wilbur (1976)
	Louisiana	Lynch and Martin, unpubl.
	Texas	Malcolm and Cockrell, unpubl.
	Kansas	Malcolm and Cockrell, unpubl.
amplexicaulis	Florida	Brower, Cockrell, and Malcolm, unpubl.
	Illinois	Price and Willson (1979)

TABLE 1. Continued.

Asclepias species	Location	Reference
	Texas	Malcolm and Cockrell, unpubl.
	Louisiana	Malcolm and Cockrell, unpubl.
	Oklahoma	Malcolm and Cockrell, unpubl.
tuberosa	Florida	Brower (1961, 1962)
	Illinois	Price and Willson (1979)
	Michigan	Wilbur (1976)
verticillata	Illinois	Price and Willson (1979)
	Kansas	Malcolm and Cockrell, unpubl.
	Minnesota	Malcolm and Cockrell, unpubl.
exaltata	Michigan	Wilbur (1976)
	Virginia	Malcolm and Cockrell, unpubl.
variegata	Texas	Malcolm and Cockrell, unpubl.
purpurascens	?	Urquhart (1960)
	Kansas	Malcolm and Cockrell, unpubl.
lanceolata	?	Urquhart (1960)
	Florida	Brower, unpubl.
sullivantii	?	Urquhart (1960)
oenotheroides	Texas	Lynch and Brower, unpubl.
fascicularis	California	Dixon et al. (1978)
eriocarpa	California	Brower et al. (1982)
speciosa	California	Brower et al. (1984b)
californica	California	Brower et al. (1984a)
erosa	California	Brower et al., in prep.
cordifolia	California	Brower et al., in prep.
vestita	California	Brower et al., in prep.

predators (Brower 1984), cardenolides may be implicated in some form of host selection.

To test host selection by *D. plexippus* between *Asclepias* species, based on biomass and cardenolide measures, we counted the numbers of monarch eggs and larvae on plants within a mixed stand of two *Asclepias* species, *A. curassavica* and *A. incarnata*, that are known to have different cardenolide concentrations (Roeske et al. 1976).

METHODS

The study site was a large mixed stand of *A. curassavica* and *A. incarnata* in a wet pasture adjacent to a man-made lake 15 km NW of Miami, Dade Co., Florida (25°45′N, 80°22′W, near junction of highways US-27 and I-95). On 1 and 2 September 1984, six 10 m × 10 m, randomly selected plots were searched and the following measurements made: 1) number of plants per plot, 2) plant height, 3) number of stems per plant, 4) presence of flower buds and flowers (no seed pods were found), 5) number of leaf pairs per plant (like most milk-

TABLE 2. Leaf cardenolide concentration and plant size of five milkweed species in May 1983 and 1984 within 25 km of Gainesville, Florida.

Asclepias species	Cardenolide concentration (μg/0.1 g dry leaf) Mean	SD	Range	N	Mean dry leaf biomass/plant (g)
Common					
humistrata	471	157	182–797	29	7.8
viridis	478	136	316–676	7	12.5
verticillata	14	—	—	1	<0.1
Occasional					
amplexicaulis	3	3	0–6	4	1.2
tomentosa	15	12	6–23	2	1.8

weeds these two species have opposite leaves), and 6) numbers of monarch eggs and larvae by instar. All eggs were collected and kept until larval emergence to determine whether they were *D. plexippus* or the queen, *D. gilippus*. The three eggs on *A. curassavica* and one on *A. incarnata* that proved to be queens were excluded from the analysis. Arbitrarily selected leaf samples were also collected from five plants of each species to measure leaf length, width and dry weight. These dried leaves were ground, mixed, and 0.2 g of each species extracted with ethanol to estimate their cardenolide concentrations by spectroassay (Brower et al. 1975, 1984b).

RESULTS

The cardenolide concentration of *A. curassavica* leaves was 864 μg cardenolide/0.1 g dry leaf, and that of *A. incarnata* 24 μg cardenolide/0.1 g dry leaf. Thus *A. curassavica* at this location had, on average, 36 times more cardenolide than *A. incarnata*.

The six 100 m^2 plots contained 182 *A. curassavica* plants, with 430 stems on which 33 monarch immatures were found, and 77 *A. incarnata* plants, with 393 stems bearing 11 immature monarchs, distributed between the plots as shown in Table 3.

The two milkweed species are very similar in appearance, bearing similar sized, lanceolate leaves. Neither leaf length, width, or shape (length/width) of the two species were significantly different (Table 4a), but the dry leaves of *A. incarnata* were significantly heavier than *A. curassavica*. Since *A. incarnata* plants were significantly taller with more stems per plant than *A. curassavica* (Table 4a), they also had significantly more leaves (Table 4b). Thus each *A. incarnata* plant had greater biomass available to monarch larvae than *A. curassavica*. However there were more than twice as many *A. curassavica* than *A. incarnata* plants per 100 m^2 (Table 4b), which resulted in similar num-

TABLE 3. Distribution of immature monarchs on six 100 m^2 plots in a mixed stand of *A. curassavica* and *A. incarnata* near Miami, Florida, on 1 and 2 September 1984.

				No. of insects						
					Instar no.					
Plot no.	*Asclepias* species	No. plants	No. stems	Eggs	1	2	3	4	5	Total
1	*curassavica*	34	92	6	—	2	—	—	—	8
1	*incarnata*	13	86	1	—	—	—	—	1	2
2	*curassavica*	62	162	6	—	1	—	—	—	7
2	*incarnata*	16	89	—	—	—	—	—	—	0
3	*curassavica*	17	44	1	—	1	—	—	—	2
3	*incarnata*	8	43	—	—	1	—	—	—	1
4	*curassavica*	31	69	5	—	—	—	—	—	5
4	*incarnata*	6	36	1	—	—	—	—	—	1
5	*curassavica*	17	27	—	—	1	—	—	—	1
5	*incarnata*	18	66	—	—	1	—	—	—	1
6	*curassavica*	21	36	4	3	2	—	—	1	10
6	*incarnata*	16	73	5	—	1	—	—	—	6
Total	*curassavica*	182	430	22	3	7	—	—	1	33
Total	*incarnata*	77	393	7	—	3	—	—	1	11

bers of stems overall (Table 3, t = 0.28, P = 0.78 NS) with almost equal leaf density and dry leaf biomass of each *Asclepias* species available to ovipositing monarchs (Table 4b).

Despite the similarity of the leaf biomass for each milkweed species, three times the number of immature monarchs (eggs to fifth instars) were found on *A. curassavica* than on *A. incarnata* (Table 4b). Similarly, when numbers of monarch immatures are corrected for host biomass, there were more than five times the number of monarch immatures/dry leaf mass on *A. curassavica* than on *A. incarnata* (Table 4b).

The difference between the numbers of monarch immatures on the two *Asclepias* species is unlikely to be explained by flower attraction since significantly more *A. incarnata* plants (with fewer monarch immatures) were flowering than *A. curassavica* (Table 4b), although most plants of both species were flowering.

DISCUSSION

We suggest that our observation of significantly more immature monarchs/leaf mass on *A. curassavica* than on *A. incarnata* may be explained by the 36 times greater cardenolide concentration of *A. curassavica* over *A. incarnata*. These results contrast with those reported by Dixon et al. (1978) who suggest that monarchs oviposit on *Asclepias* species with the lowest cardenolide concentrations. They found that

TABLE 4. Plant characteristics of *A. curassavica* and *A. incarnata* on six plots in a mixed stand at the study site near Miami, Florida, on 1 and 2 September 1984. Differences were tested at the 0.05 level.

a) Leaf measurements and plant height

Asclepias species	Leaf length (mm)	Leaf width (mm)	Leaf length/width	Leaf dry weight (mg)	Plant height (cm)	No. stems/plant
curassavica						
Mean	81.1	14.2	5.8	34	70.5	2.4
SE	2.5	0.6	0.2	2	1.1	0.1
N	20	20	20	20	182	182
incarnata						
Mean	91.6	15.1	6.3	55	91.1	5.1
SE	5.8	1.0	0.4	9	1.8	0.4
N	18	18	18	18	77	77
t	1.6	0.9	1.0	2.2	9.8	8.1
df	24	36	26	20	257	257
P	0.06	0.20	0.16	0.02	0.0001	0.0001

b) Mean plant measurements and monarch numbers per 100 m²

Asclepias species	No. plants	Percent flowering	No. leaves/ plant	No. leaves/ plot	Leaf dry mass (g)	No. immature monarchs	No. monarchs/ leaf mass
curassavica							
Mean	29.2	64	35.2	1,143	38.5	5.5	0.17
SE	7.1	7	2.9	334	11.2	1.4	0.06
N	6	6	6	6	6	6	6
incarnata							
Mean	12.8	90	88.2	1,130	62.5	1.8	0.03
SE	2.0	5	8.3	190	10.5	0.9	0.01
N	6	6	6	6	6	6	6
t	2.2	2.9	6.0	0.03	1.6	2.2	2.2
df	6	10	7	10	10	10	5
P	0.03	0.01	0.001	0.49	0.07	0.03	0.04

D. plexippus laid more eggs on *A. curassavica*, with a cardenolide concentration of 56 μg/0.1 g dry leaf, than on *Gomphocarpus fruticosus*, with 63 μg cardenolide/0.1 g dry leaf. However, their cardenolide concentrations are too similar to reach any conclusion as to cardenolide-based oviposition preference, particularly as they are the same cardenolide determinations first reported as "approximate amounts ±50%" (Rothschild et al. 1975), and were not determined for the same plants used in their oviposition experiments. *Gomphocarpus fruticosus* is also an African milkweed species which casts doubt on experimental relevance, since monarch butterflies will only encounter recently introduced plants of this species in Australia. Using Australian *D. plexippus*, Zalucki and Kitching (1982) also found that females preferred to lay eggs on *A. curassavica* rather than on *A. fruticosa* (=*G. fruticosus*); but citing different published data on cardenolide concentrations (Roeske et al. 1976), they suggested the reverse, that monarchs laid eggs on the milkweed species with most cardenolide.

The use of milkweed-derived cardenolides appears to be at least a partial defense against wild avian predators for adult monarchs overwintering in Mexico (Fink & Brower 1981, Fink et al. 1983, Brower & Calvert 1985, Brower & Fink 1985). It is likely that monarchs in south Florida also benefit from cardenolide-based protection against bird predators, particularly as late summer bird migrants pass through south Florida.

Although we recently found that monarchs regulate their cardenolide concentrations by increasing or reducing the cardenolide concentrations from their larval host plants, milkweeds such as *A. incarnata* have insufficient cardenolide from which monarchs can concentrate an effective cardenolide-based defense. For example, although monarchs reared on *A. speciosa* can almost double their cardenolide concentrations relative to those of host plants, from 90 to 179 μg/0.1 g (Brower et al. 1984b), this concentration is less than the concentrations in butterflies reared on other species of cardenolide-rich milkweeds. Roeske et al. (1976) found that adult monarchs reared from *A. curassavica* reflect the high cardenolide concentration of their host leaves, in this case of 386 μg/0.1 g dry leaf, with a concentration of 319 μg/0.1 g dry butterfly. In contrast, they found monarchs reared from *A. incarnata* with 0–28 μg cardenolide/0.1 g had between 28 and 127 μg cardenolide/0.1 g dry butterfly. The emetic response of bird predators increases with cardenolide concentration above a lower threshold dependent on cardenolide polarity (Roeske et al. 1976). Thus monarchs that fed on *A. curassavica* as larvae at our site near Miami will be much better protected by cardenolides against bird predators than monarchs that developed on *A. incarnata*.

Since individual plants of both species have a mean dry biomass sufficient to support the development to pupation of at least one monarch larva (between 0.92 g and 1.74 g dry leaf is required [Schroeder 1976, Dixon et al. 1978]; *A. curassavica* has $0.034 \times 35.21 = 1.20$ g, and *A. incarnata* has $0.055 \times 88.23 = 4.87$ g [Table 4]) a monarch larva need not move from plant to plant, either within, or between the two milkweed species. Thus the effectiveness of cardenolide-based monarch defense is likely to be determined primarily by the oviposition behavior of the adult female rather than by larval movements, particularly in view of the unpredictable costs and benefits of such larval movement between milkweeds (Borkin 1982). Unlike Borkin, we do not find instars 2 and 3 moving between plants in Florida. If late instars move between plants, they are more likely to find another *A. curassavica* plant. Their feeding experience may also ensure that they keep moving until they find another host plant of the same species.

Cardenolides are unlikely to be the sole determinant of host selection in these observations. Other explanations of the observed oviposition bias for *A. curassavica* include 1) females may in some way be able to perceive a nutritional superiority of *A. curassavica* over *A. incarnata* (Erickson 1973); 2) monarch females may be more attracted to the orange and yellow flowers of *A. curassavica* than the pink flowers of *A. incarnata* (however, in central Florida monarchs preferred to oviposit on the pink flowered *A. humistrata* compared to the orange flowered *A. tuberosa* (Brower 1961, 1962)); and 3) females may have responded to the number of plants available for each species (Table 3) rather than to the similar quantities of stems, leaves, and leaf biomass.

Nevertheless, whatever the explanation, the natural experiment described in this paper as well as the observations reported by Brower (1961, 1962) are evidence for the oviposition preference by monarch butterflies for cardenolide-rich milkweed species. We suggest that this choice may be the result of natural selection having favored a discriminatory mechanism allowing adult female monarchs to choose milkweed species that provide their offspring with a more effective cardenolide-based defense against predators.

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