SOME DIFFERENCES BETWEEN TEMPERATE AND TROPICAL POPULATIONS OF MONARCH *(DANAUS PLEXIPPUS)* AND QUEEN *(DANAUS GILIPPUS)* BUTTERFLIES (LEPIDOPTERA: DANAIDAE)[1]

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This report concerns some preliminary studies on the comparative population structure and incidence of parasitism by tachinid flies (Tachinidae) in temperate and tropical populations of the Monarch Butterfly, *Danaus plexippus*, and the Queen Butterfly, *Danaus gilippus* (Lepidoptera: Nymphalidae: Danainae). Various aspects of population structure and mortality from tachinids are given for one mixed tropical population of Monarchs and Queens during wet and dry seasons, and lesser data of this sort are summarized for two temperate populations of the Monarch alone. From these findings the testable hypothesis is advanced that tropical populations of these ecologically similar butterflies should, on the average, (1) suffer from higher amounts of biotic mortality, especially on immature stages, than comparable temperate populations, and (2) further studies should reveal that Monarchs and Queens in the tropics are biologically-accommodated species while physically-controlled species at northern latitudes.

METHODS

Intermittently during the period March 1969 through April 1970, censuses of oviposition and caterpillars of both butterflies were taken in a small (approximately 400 m^2) field containing an abundance of *Asclepias curassavica* (Asclepiadaceae), a larval food plant of both butterflies, in northeastern lowland Costa Rica. In my experience, both species are unusually abundant at this site, which is just southwest of La Virgen (about 10^{o} 26'N Lat; 90 m elev.) and along the road going to the neighboring town of Puerto Viejo. But the third species of *Danaus* known to occur in Costa

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Rica, namely, *D. eresimus,* was absent during this study at this site. Census of ovipositing females and caterpillars was limited to this patch. Through census of ovipositing adults, eggs on *A. curassavica,* and caterpillars in this patch, I hoped to obtain some descriptive data on the populations of these butterflies. Both adults and caterpillars are easy to speciate in the wild, but this cannot be easily done with eggs. Therefore, the relative abundance of eggs between the two species discussed in this paper refer only to eggs actually witnessed to be oviposited, and not to eggs discovered on plants.

In order to estimate relative abundance of the adults on a given day, I counted the number of each seen during a 15-minute interval. As the patch is low with all parts of it easily visible, it was possible to keep tract of most of the butterflies in it for 15 minutes or less.

During the census of caterpillars, fifth instars were usually collected and brought into the laboratory to complete ontogeny. Their pupae were then scored for frequency of parasitic attacks. Earlier, I had discovered that pupae of both species are killed by larvae of at least two species of Tachinidae in this general region of Costa Rica. The caterpillars of both species are apparently infected with larvae of two tachinid genera: *Hyphantrophaga* and *Patelloa* (with both of these being undescribed species – Dr. Curtis W. Sabrosky, pers. comm.). In my experience the larvae of these two parasites seldom reach maturity prior to the pupa state in both butterflies. Thus by censusing the pupae from caterpillars brought in from the wild in late fifth instar, I hoped to obtain estimates of mortality rates on both species by scoring for pupae bearing flies. The caterpillars were kept separate by species in clear plastic bags containing sprigs of *A. curassavica* that was refreshed until pupation.

Other studies summarized here include observations on densities of immatures and incidence of parasitism in two temperate zone population of the Monarch: one of these, located along a roadside (Stony Island Ave.) in south Chicago, was censused during August and September of 1966, and the other located in an old field in Appleton, Wisconsin was sampled during September 1971. Approximately the same number of days were spent sampling eggs and caterpillars (by instars) at these localities. The area of dense

Asclepias syrica sampled in Appleton was 400 m^2, in Chicago, the area was 400 m^2, and in Costa Rica, 396 m^2. These areas were used to calculate densities. The species of *Asclepias* in the Chicago plot was not identified. Both temperate sites support Monarchs in abundance.

RESULTS

Both butterflies occur regularly at the study site, in Costa Rica although there is a decline of adults during the drier months (Table 1). The dry season in this region of Costa Rica is very variable in both duration and intensity (dryness) in different years, as seen from the accurate weather records for La Virgen provided by the Servicio Meteorologico de Costa Rica. But a dry season generally falls between January and April. The Queen is never as abundant as the Monarch, and the source of this difference remains obscure at the present (Table 1). As the numbers of both Monarch and Queen caterpillars in this field are rather comparable (Table 2),

Table 1. Summary of adult numbers of the Monarch Butterfly *(Danaus plexippus)* and the Queen Butterfly *(D. gilippus)* seen in 15-minute sightings (once per day)[a] over a large patch of *Asclepias* sp., near La Virgen (de Sarapiqui) Costa Rica, 1969-1970.

NUMBERS OF ADULT:

Months	N[b]	Monarchs (mean ± S.E.)	Queens (mean ± S.E.)
March, 1969	2	3 ± 0.0	2 ± 0.0
April	3	5 ± 0.5	2 ± 0.4
May	2	22 ± 2.0	6 ± 0.0
June	3	31 ± 2.4	13 ± 0.8
July	3	28 ± 3.0	10 ± 0.6
August	2	25 ± 2.4	10 ± 1.0
September	4	27 ± 3.0	12 ± 0.4
October	2	30 ± 2.0	9 ± 0.4
November[c]	2	24 ± 1.4	10 ± 0.2
January, 1970	3	5 ± 0.2	2 ± 0.0
February	1	2 ± 0.0	0 ---
March	2	4 ± 0.0	1 ± 0.0
April	3	5 ± 0.2	5 ± 0.0
May	3	19 ± 1.0	13 ± 0.0
June	2	25 ± 2.0	11 ± 0.4

[a]Censusing was conducted at the same time (10:00 A.M. – 1:00 P.M. C.S.T.) on different days.

[b]N is the number of days each month on which adults were censused.

[c]No data are available for December, 1969

the discrepancy in adult numbers between the species may reside in some somponent of the adult ecology. A decline of the adults in both species during the drier months may be due in part to a reduction in recruitment of new individuals as reflected in the paucity of caterpillars during these months (Table 2).

The oviposition activity of both butterflies is high in this field, but once again with a noticeable reduction during the dry season (Table 3). It thus appears that the general decline in the mixed population of these two butterflies during the dry season results from a reduction in egg-laying in the field due to fewer adults being present. But it is not known if there is an increased mortality of adult butterflies during this period, or whether adults emigrate to wetter sites in this region. Differential mortality of immatures for both butterflies here but in different seasons likewise cannot be ruled out here as a factor causing population decline.

The estimations of densities of immatures in both temperate and tropical regions indicates that there are no major shifts associated

Table 2. Summary of the relative abundance of Monarch and Queen caterpillars[a] in a large roadside patch of *Asclepias* sp., near La Virgen (de Sarapiqui), Costa Rica, 1969-1970.

		NUMBERS OF LARVAE:	
Months	N[b]	Monarchs (mean ± S.E.)	Queens (mean ± S.E.)
March, 1969	4	0	0
April	5	0	0
May	3	7 ± 0.0	5 ± 0.0
June	5	18 ± 2.2	20 ± 1.0
July	6	33 ± 4.0	23 ± 1.0
August	3	45 ± 3.0	29 ± 0.5
September	4	50 ± 3.5	12 ± 0.0
October	6	41 ± 3.0	21 ± 0.0
November	2	35 ± 1.0	18 ± 1.0
January, 1970	3	22 ± 1.0	20 ± 1.0
February	5	0	1 ± 0.0
March	4	2 ± 0.0	0
April	4	38 ± 1.0	22 ± 1.0
May	5	35 ± 2.0	25 ± 2.0
June	2	30 ± 1.5	20 ± 1.0

[a]Excluding first and second instars

[b]N is the number of days of census in each month.

with latitude for the populations studied (Table 4). Densities of eggs on food plants in butterflies is the result of several factors including (1) the pattern of movement of the ovipositing females, (2) the spatial availability of the food plant used for egg-laying, (3) the number of eggs a female produces, and (4) the rate of egg-laying. The movement patterns of temperate and tropical Monarchs are very similar, involving an erratic searching flight over a field, and the spatial distribution of *Asclepias* in both situations is also similar, with large clumps of individual plants distributed over the field. And temperate and tropical females have the same number of eggs as teneral adults: 63 females dissected from the Appleton population gave an average of 54 $\pm$ 6.2 eggs ($\bar{X} \pm$ S.E.), and 49 females from the Costa Rica site gave an average of 59 $\pm$ 8.3 eggs. The rates of egg-laying are not known, and with this exception, we can predict that egg density might be very similar since the other factors contributing to egg density on food plants are similar for the populations studied. The apparently high density feature of these populations contributes to conditions favorable to substantial attack by parasitic tachinids at least in the tropics (Table 5). But such mortality is absent in both Chicago and

Table. 3. The relative numbers of eggs witnessed being oviposited[a] by Monarchs and Queens.

Months	N[b]	Monarch eggs	Queen eggs
March, 1969	2	3	0
April	3	6	0
May	2	16	12
June	4	38	43
July	4	13	30
August	2	20	19
September	4	12	30
October	5	40	26
November	5	33	40
January, 1970	3	11	47
February	1	2	4
March	2	5	3
April	2	40	38
May	3	38	29
June	3	44	42

[a]Observations on oviposition sequences of Monarchs and Queens were made for a 45-minute period on each day.

[b]N is the number of days each month that oviposition was censused.

Appleton populations of the Monarch, although this might be attributed to sampling error. At least two genera of tachinid flies contribute equally to the mortality of pupae observed for the Monarch and Queen tropical populations (Table 6).

Table 4. Average densities[a] of immature life stages for the Monarch butterfly, *Danus plexippus* in Costa Rica (La Virgen), Illinois (Chicago), and Wisconsin (Appleton).

			mean numbers (per ft^2) with standard errors (I.S.E.):					
LOCALITY	SAMPLING PERIOD	N[b]	EGG	INSTAR-1	INSTAR-2	INSTAR-3	INSTAR-4	INSTAR-5
COSTA RICA	APR-JUNE 1970	18	1.2+0.4	0.82+0.03	0.80±0.04	0.75±0.06	0.20+0.05	0.13+0.04
ILLINOIS	SEPT-OCT 1966	13	1.4+0.3	1.1±0.09	1.0+0.03	1.0±0.06	0.9±0.07	0.9+0.05
WISCONSIN	SEPT-OCT 1971	16	1.8±0.4	1.6±0.04	1.5+0.02	1.2±0.04	1.2+0.05	1.1±0.07

[a]Averages computed from a specified number of days of sampling within the "sampling periods" given in the table.

[b]N is the number of days used to compute average densities of life stages.

Table 5. Relative frequencies of pupal mortality due to parasitic attack by *Hyphantrophaga* sp. and *Patelloa* sp. (combined data) in sympatric larval populations of the Monarch and Queen butterflies.

	Monarch Butterfly			Queen Butterfly		
Monthly samples[a]	Total No. of pupations	No. pupae yielding flies	% mortality	Total No. of pupations	No. pupae yielding flies	% mortality
March, '69	0	-		0	-	
April	0	-		0	-	
May	5	3	60%	5	4	80%
June	16	9	56%	20	16	80%
July	33	17	52%	23	18	78%
August	43	14	33%	28	12	43%
September	48	22	47%	10	6	60%
October	41	22	54%	17	10	59%
November	32	18	57%	18	14	77%
Jan., '70	22	19	86%	20	12	60%
February	0	-	-	1	1	100%
March	1	1	100%	0	-	-
April	36	24	67%	20	15	75%
May	35	19	54%	25	15	60%
June	30	17	57%	18	14	78%

[a]These refer to the numbers of fifth instar larvae collected in the wild and allowed to pupate in the laboratory.

Table 6. Relative contributions of two tachinid parasites, to the overall mortality of pupae in tropical populations of the Monarch and Queen butterflies.

Parasite	% pupal mortality in a Monarch population	% pupal mortality in a Queen population
Hyphantrophaga sp.	34%	37%
Patelloa sp.	28%	31%

DISCUSSION

Both the Monarch and Queen in Costa Rica apparently occupy very similar ecological niches, being congeners, and this clearly includes their susceptability to parasitism by some tachinids. The caterpillars of both species feed on the same food plant, and such food selection might make it easier for adult parasitic flies to locate the "correct" plants for egg deposition, a condition studied in other insect host-parasite associations and involving a chemical cue from the plant (Read, Feeny, and Root, 1970). It is generally known the certain dipterous parasites of Danaid butterflies lay their eggs on leaves of the plants and from there parasitize the caterpillars. Too little is currently known about the natural history of *Hyphantrophaga* and *Patelloa* tachinid flies to know if this is the case here. Both species appear to be non-discriminatory between Monarch and Queens, and we might predict that selection would favor dipterous parasites to be "generalists" in the tropics since any one host on the average may be rarer and a fly will lose more energy in being species-specific under these conditions. Thus we might predict that species in different tachinid genera and other parasitic dipterous families are non-specific in host preference, and such a feeding strategy would be well suited in species that lay their eggs on plants and other substrates rather than directly on the bodies of their hosts. In this way, eggs could be ingested by a variety of herbivorous insects on a given plant species and given the proper range of internal physiological conditions in hosts, a good proportion of eggs may survive to produce new adults. The toxic properties of *Asclepias* (see Ehrlich and Raven, 1964 for comments) may make it a very suitable "candidate" plant species for a variety of tachinid flies to cue into by olfaction and allow them to infest several lepidopterous, coleopterous, and hemipterous herbivores that are able to feed on these milkweeds.

The size of the study site is large enough to support breeding (egg-laying) populations of both butterflies and this is very likely due to the abundance of *Asclepias* plants found there. As data were not recorded on seasonal patterns of flowering in this plant nor on any deciduous response to the dry season, it is difficult to pin down the causes of population decline at this time. Adults of both species feed primarily on nectar of *Asclepias* in this field. Although many woody trees and shrubs bloom during the tropical dry season (Janzen, 1967) little has been published on seasonality of flowering in secondary growth herbaceous forms. The toughness and succulent properties of *Asclepias* plants suggests that they do not become leafless during the moderate to weak dry season characteristic of this region of Costa Rica, thus suggesting the larval food does not become scarce. But I have noticed qualitatively that milkweed blooming is greatly reduced during the dry season in this field. This has two impacts on the Monarch-Queen populations here: (1) a highly preferred adult food source becomes scarce, and (2) the likelihood of oviposition in the field is also reduced. This second prediction stems from the observation of Brower (1961) that young blossoming milkweeds are more likely to have eggs than either young or old plants not in bloom. Brower suggests that the blossom serves a visual stimulus that is *Asclepias*-specific for Monarchs. But such a mechanism may not be operative in the northern spring breeding populations of the Monarch. On June 12, 1971 I censused 244 very young *A. syrica* plants in one field in Appleton for Monarch eggs; none of these very small plants (average height about 25 cm) had blossoms. Out of the 244 plants surveyed, 63 or 25.8% had at least one Monarch egg. There were only two plants with two eggs apiece, and the total number of eggs was 65, of which 26 or 40% were oviposited on the dorsal leaf surfaces. No caterpillars were present and the young *A. syrica* plants were often covered with various ant species.

Further studies are needed to explain seasonal patterns of population age-structure and numerical abundance. Increased dryness may also cause adults to become subject to dessication in open fields and cause them to move into wetter sites. The paucity of immatures on *Asclepias* during the drier months at this site suggests that adults previously left the area, but increased mortality of immatures during the dry season cannot be ruled out. The problem of dry season effects on populations even becomes more complex in more seasonal Costa Rican environments: On March 8, 1970, I observed many fresh adults of the Queen at Palo Verde, near the Rio Tempisque in Guanacaste Province, a tropical dry forest region, and at the same time there were only a few very old Monarchs in the same area. In this situation it appears that the species are responding differently to the severe dry season of this region if seasonality is affecting population age-structure.

In light of the apparent similarities in densities of immatures among temperate zone and tropical populations of the Monarch, it is extremely interesting that tachinid parasitism should be high in the tropics and virtually non-existent in the temperate populations. If we assume for the moment that the very limited data given here are in fact representative of a general latitudinal trend, then it appears that tropical Monarch populations during the "growing season" experience greater mortality from tachinid parasitism than do similar temperate zone populations. Such a latitudinal pattern may also be true for the Queen. If this is true, then we might predict that selection increases the vagility of adults in tropical populations as a means of escaping in space from parasitism through colonization of new food plant patches, assuming that other mortality factors are held constant. This discussion assumes that no other biotic mortality factors are killing immatures of Monarchs or Queens in temperate areas – an assumption that may be faulty since the eggs and younger caterpillars may be parasitized by other parasites and predators. The total spectrum of biotic mortality on immatures in both temperate and tropical populations of the butterflies should be investigated in order to substantiate this hypothesis.

In closing, I have found that large numbers of young Monarch caterpillars are killed off during early or middle October in Appleton each year, although quantitative estimates of this mortality are not determined. The mortality corresponds with the date of the first killing frost, which from 1959 through 1970, generally occurs within the first three weeks of October in Appleton. The average date is October 17, and the range is October 5 to October 29. Variability of the date of the first killing frost within the three weeks period is difficult to label as being predictable or unpredictable from year to year, but I suspect that it might be the latter owing to Monarchs having a developmental time of more than three weeks. Although some years are "exceptional" for Monarchs, presumably resulting from an unseasonally late first killing frost date and allowing many more young Monarchs to successfully complete development, the unpredictability of this environmental factor results, on the average, in large numbers being killed off. Thus temperate populations of Monarchs are at least in part physically-controlled by killing frost. It is less likely that comparable mortality from climatic instability would occur in the Costa Rican population studied through a dry season effect. If we may extend this speculation further, temperate zone populations of Monarchs, especially those far north, are physically-controlled while tropical populations are biologically accommodated (Slobodkin and Sanders, 1969) with part of the latter including high rates of parasitism. Clearly we need more data from several populations along a latitudinal gradient to confirm some of these ideas; butterflies like Monarchs and Queens are especially suited for such studies owing to (1) the widespread latitudinal occurrence of both from temperate-zones to the tropics, and (2) their apparent dependence upon Asclepiadaceae as larval food plants.

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ABSTRACT: A mixed population of Monarch and Queen butterflies was investigated intermittently over several months in a small field of *Asclepias curassavica* (Asclepiadaceae) in northeastern lowland Costa Rica. Ecological parameters measured included number of adults of both species seen on selected days, frequency of oviposition in both species, numbers of caterpillars of both species on *A. curassavica*, and the number of pupae producing *Hyphantrophaga* and *Patelloa* parasitic flies (Tachinidae) from fifth instar caterpillars brought into the laboratory. These studied extended over both wet and dry seasons. In addition to this Costa Rican site, densities of immatures for the Monarch were also studied in Illinois (Chicago) and Wisconsin (Appleton), and examinations for parasites in caterpillars and pupae were also conducted. The Costa Rican field supported roughly equal numbers of Monarchs and Queens and there was a very sharp decline in adults during the dry months, perhaps due to an exodus of butterflies since the frequency of oviposition also dropped severely. Although larval densities in the temperate zone and tropical populations of the Monarch were very similar, both the Monarch and Queen in Costa Rica suffer very high levels (about 60%) of mortality from tachinids while none was found in Illinois and Wisconsin. The hypothesis is advanced that tropical populations of these butterflies are biologically-accommodated and suffer high levels of biotic mortality while temperate populations are physically accommodated. Allen M. Young, Department of Biology, Lawrence University, Appleton, Wisconsin, 54911.

Descriptors: Monarch, Queen, butterflies, populations, temperate, tropical, parasitism, Tachinidae, biologically-accommodated, physically-controlled, environment.

ERRATA

Vol. 85 (1) January, 1974 – Cover – A New Genus and Species of Mealbug should read Mealybug.

p. 30 – References: This should follow article on p. 28 "Population and Subspecific Variation in *Gerris Remigis* Say."