

Host specialization of satyrine butterflies, and their responses to habitat fragmentation in Trinidad

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Introduction

Butterflies may be among the most useful indicators of habitat change (Ehrlich & Murphy 1987, Kremen 1992). In this paper we describe the communities of grass- and sedge-feeding Satyrinae (Nymphalidae) butterflies from ten study sites in Northern Trinidad in 1970-74, and assess the extent to which species may have been lost as a result of human modification of the landscape. In undisturbed habitats such as still exist in some neotropical countries, satyrines move through the forest, feeding as adults on fallen fruit, and ovipositing on patches of grass or sedge that grow at treefalls or beside streams (DeVries 1985;1987). Although the patches of larval habitat may be widely scattered, there are few obstacles to the movement of adults. In contrast, human disturbance increases host plant abundance and decreases patchiness, but creates obstacles to the movement of adults, most of which will not fly through open areas. Thus, the clearing of tropical forests in Northern Trinidad has resulted in considerable fragmentation of habitat for these shade-loving species. The resultant reduction in population sizes could cause local extinction of specialist insects from the habitats that still contain their hosts. We seek evidence for such local extinction by comparing the distributions of these insects with the fragmented distributions of their hosts. We also compare our data with historical records gathered by Barcant (1970) to ask whether there is evidence for recent extinction of either specialist or generalist species from the Island of Trinidad.

As a prerequisite for this work we needed to classify the study species as either host specialists or host generalists, since no information on their diets was previously available. We also obtained information on host plant species richness and abundance, and asked whether either of these traits was correlated across habitats with either butterfly species richness or butterfly abundance.

Study Species

The generic status of many of the neotropical Satyrinae is unclear (see discussion in DeVries 1987). For the purposes of this paper we have placed all satyrines studied here in the genus *Cissia* since many of them, including *palladia*, *terrestris*, *myncea*, *libye*, *themis* and *penelope*, are very likely to belong in this genus (Singer et al. 1983; DeVries 1987).

Satyrine butterflies are known to feed on various monocotyledonous plants including palms and Marantaceae as well as grasses and sedges

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(DeVries 1987). A small group (the genus *Euptychia*) has colonized lower plants, feeding on *Selaginella* (Singer et al. 1983) or on epiphytic mosses (Singer & Mallet 1975). However, the Trinidadian species we studied were restricted to grasses and sedges in their diets. Observations of oviposition on other plants, including *Selaginella*, turned out to be examples of oviposition away from the host plant by insects whose larvae were unable to feed on the plants that actually received eggs (Singer et al. 1971).

Satyrine butterflies are, to varying degrees, shade-loving insects. Among our study insects, *arnaea*, *myncea* and *junia* were the most shade-loving, while *hermes*, *themis* and *penelope* were the least restricted to deep shade. This trait is important, since the most shade-loving species should be the least able to colonize small habitat patches. In the fragmented landscape of Northern Trinidad, such colonization would usually require crossing open areas inimical to these insects.

Study Sites

Our study sites were all situated in Northern Trinidad. All but two, "Trace" and "Trace Plantation," were close to sea level. "Trace" was an ill-kept trail along a ridge-top through montane rain forest at about 800 m elevation. "Trace Plantation" was an abandoned, heavily-shaded and overgrown cacao plantation at the same elevation. "Guanapo" was a cultivated flat with bananas, cocoa, and coffee. "Dump 1" and "Dump 2" were adjacent sites close to Guanapo town dump. "Dump 1" was entirely second growth, with few shrubs more than ten feet high, while "Dump 2" was less recently disturbed and quite heavily shaded. "Cave" was another abandoned and overgrown Cacao plantation, at much lower elevation than "Trace Plantation". The remaining four sites were all in the city of Port of Spain in a well-preserved patch of dry forest just North of the Zoo. The sites coded as "POS 1, POS 2, and POS 3" were very close together, separated from each other by uncensused strips only about 50 m wide that also contained butterflies.

With the exception of "Trace", which was an elongated study site bordering a trail, all of our study sites were approximately rectangular. Most were on the order of 10,000m² in area, but "Cave", and the three "POS" sites were about half this size.

Habitat fragmentation in Northern Trinidad was already extensive at the time of this study (1970-74), and no substantial patches of forest remained in our study area. The two "dump" sites were each separately cut off from suitable habitat, as were the three "POS" sites as a group. Only the least shade-restricted species would now have easy access to these sites. The "Guanapo" site was surrounded by habitat that was not totally unsuitable but sufficiently open that the more shade-loving species were reluctant to travel through it. All other sites were at least partially connected to shaded habitat through which adult insects could travel.

Methods

Standard counts of adult butterflies were performed in timed searches of the habitats (cf Pollard (1977)). No habitat was sampled twice in any morning or afternoon, but some were sampled twice in the same day. No habitat was sampled less than three times in all, and each habitat was sampled at least once in both wet and dry seasons.

The census of the grasses was done by counting the number of species present and assigning each habitat to a category of overall grass abundance ranging from 1 (grasses averaging less than one ramet per 10 m² and nowhere abundant) to 5 (grasses providing almost complete ground cover).

Host specificity of the insects was investigated by several methods. For abundant species, we obtained direct evidence by observing ovipositions in the field, and by finding eggs and larvae and recording their hosts. For three of the rare species, we were not able to find early stages, so had to resort to indirect methods. These were:

1) Oviposition preference trials on captive adults. Insects were deprived of opportunity to oviposit for 24 hours. They were then offered sequential trials with each species of grass or sedge from their natural habitats. At each trial, the insect was placed gently on the plant and its response (oviposition or not) recorded. The range of plants accepted was classified as the host range of the butterfly. These crude trials are likely to overestimate the natural host range because of the high oviposition motivation of tested insects (Singer 1986). One species (*arnaea*) was not amenable to the trials, failing to duplicate normal oviposition behavior after manipulation. We obtained data from this species by holding females captive until oviposition motivation was high, then releasing them and observing acceptances and rejections of plants they encountered.

2) Feeding-preference trials on captive larvae. Larvae were placed in Petri dishes with three or four potential hosts from their natural habitats. Each plant species that was fed on was classified as part of the host range.

Figure 1: *Cissia* census data and host-plant distribution among ten study sites.

Sites are listed from top to bottom, while butterfly species are listed across the figure in the upper section (a) and plant species in the lower section (b). Figure 1a shows the numbers of each butterfly species censused at each site. For example, the census at "Trace" comprised 2 individual *palladia*, 6 *myncea*, 196 *hermes*, etc. Generalist feeders are shown at the left of the figure, separated by vertical lines from the three host specialists at the right.

Figure 1b shows the presence or absence of each plant species. Each species is indicated by a number; the names, where known, are given below. The figure is arranged as far as possible with the plant species vertically beneath the insects which feed on them. The host specialists at the right of Figure 1a, *arnaea*, *junia* and *erichto*, are each arranged above their respective hosts, grass species 13, 14 and 15. The generalists, *palladia*, *terrestris*,.....*themis*, *penelope*, are arranged above those hosts that are edible to them, species 1 through 13 inclusive. Tentative plant identifications are as follows: 1) *Lasiacis sloanei* 2) *Panicum* sp. 3) *Trypsacum* sp. 4) *Setaria paniculifera* 5) *Paspalum* sp. 6) *Paspalum conjugatum* 7) *Paspalum* sp. 8) *Paspalum decumbens* 9) *Panicum pilosum* 10) *Cyperus* sp. 11) *Scleria* sp. 12) *Panicum polygonatum*. 13) *Ichnanthus pallens* 14) probably *Panicum maximum* 15) Unidentified sedge. 16) Unidentified grass 17) Unidentified grass 18) *Bambusa vulgaris*

A

BUTTERFLY SPECIES		palladia	terrestris	oxyptate	myncea	hesione	illye	renata	hermes	alcione	themis	perelope	arnaea	julia	erichto
SITE	Trace	2			6	8	7	27	196	1		4	12		
	Trace Plantation		1		2	12	2	9	15	1			6		
	Guanapo		2		2	12	5	18	55		2	56	1		
	Dump 1				3	1	1	5	10		2	12			6
	Dump 2								8	1				5	8
	Cave					8				1		4			
	P.O.S. 1		2					3	11			10			
	P.O.S. 2		9	5	42	35	7		8	1		2	21	26	
P.O.S. 3			1	2	5		1	2	10			10			
			2	5	6	4	2	2	7	1		9			
	St. Ann's														

B

PLANT SPECIES		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
SITE	Trace	•				•			•	•	•	•	•	•					•
	Trace Plantation												•	•					
	Guanapo	•	•	•	•	•	•	•	•	•	•	•	•	•				•	
	Dump 1							•		•		•				•			
	Dump 2						•					•				•			
	Cave													•		•	•		
	P.O.S. 1									•				•			•		
	P.O.S. 2													•					
P.O.S. 3										•				•					
										•				•					
St. Ann's										•				•					
										•				•					

Acceptable to 11 Species
palladia → perelope

Inedible to Generalists
→ Inedible to All

Results

Data on host specificity, butterfly censuses and grass species richness are summarized in Figure 1. We identified eleven generalist butterflies (at left of figure) and three specialists. Thirteen grass and sedge species were edible to the generalists, and one of these, *Ichnanthus pallens*, (No. 13) was also edible to a specialist. Two grasses (nos. 14, 15) were classified as edible only to specialists.

Field searches of the three grass species (16,17,18) at the right of the figure revealed no eggs or larvae, and these plants were inedible to larvae of *arnaea*, *hermes*, *junia*, *myncea* and *hesione*. It was not possible to obtain sufficient larvae of the rarer insects to test them on all available plants, since satyrine larvae are cryptic and secretive, some of them extremely so. In consequence, our classification of these plants as inedible to all our study insects is tentative, though in accord with all data we were able to gather. Because we were not able to classify these plants as hosts of satyrines, we did not include them in any of our analyses of host diversity and abundance.

Table 1 shows the total number of butterfly and host species recorded at each site, and an index of butterfly abundance derived by simply dividing the total number of individuals by the length of time we spent in our census. Table 2 shows the same data for the community comprising only the generalist species and plants edible to generalists.

Spearman correlation coefficients and significance levels of correlation for all the data are shown in Table 3. When specialists and generalists are lumped there is no significant correlation between any of the insect parameters and any of the plant parameters. After removal of the specialists from the data (along with the plants which are edible only to these specialists) the correlation between plant abundance and insect abundance rises to a (just) significant level.

Discussion

ACCURACY OF HOST SPECIFICITY DATA

The evidence for classifying as such the generalists and their hosts is of variable quality. Classification of specificity was made from field records of oviposition and larval distribution for ten of the fifteen species we found. For four of the rare species *palladia*, *ocypete*, *alcinöe* and *erichto*, we had to rely on data from captive insects. One rare species, *cephus*, found at St. Ann's as a single specimen, gave no diet information, and may not even be grass-feeding. We accordingly omitted *cephus* from our analyses. In general, field data are better than laboratory data as indicators of specificity, since insects often show greater diet breadth in captivity than in their natural habitats (Singer 1986).

We found *hermes* larvae feeding in the field on 8 plant species, *renata* on 6, *penelope* on 5 and *hesione* on 5. Their larvae will eat all the other species if offered them though one of the sedges (No. 11) is only edible to most larvae when young. Some of these plants are sufficiently rare that

Table 1. Characteristics of plant and butterfly communities at ten sites.

Site	Butterfly Species	Butterfly Abundance	Plant Species	Plant Abundance
Trace	9	37.6	8	4
Trace Plantation	8	15.3	2	5
Guanapo	9	38.3	11	5
Dump 1	8	13.3	4	4
Dump 2	4	7.33	4	2
Cave	3	4.33	1	2
POS 1	4	8.67	2	3
POS 2	10	39.0	2	1
POS 3	7	7.00	4	2
St. Ann's	10	15.7	4	4

Table 2. Characteristics of generalist insects and their hosts.

Site	Butterfly Species	Butterfly Abundance	Plant Species	Plant Abundance
Trace	8	35.9	8	4
Trace Plantation	7	13.6	2	5
Guanapo	8	38.0	11	5
Dump 1	7	11.3	3	4
Dump 2	2	3.00	1	2
Cave	2	3.00	1	2
POS 1	4	8.67	2	3
POS 2	8	27.3	1	1
POS 3	7	7.00	4	2
St Ann's	8	9.67	3	4

we would be unlikely to have found larvae on them, even if they were high quality hosts. Among the rare insects, *alcinöe* and *themis* oviposited readily on 5 grass species offered to free-flying insects in an insectary. We were unable to obtain natural oviposition behavior from captive *terrestris*, *ocypete*, or *palladia*. Evidence for classifying these three species as generalists is poor, and consists only of recording which plant species were readily consumed by captive larvae.

We have more than 30 observations of *arnaea* feeding on plant species 13, *Ichnanthus pallens*. Our evidence for the edibility of this plant to generalists is also good: we have field observations of *hermes*, *renata*, *libye*, and *hesione* feeding on this species, and we have raised larvae of *myncea*, *alcinöe* and *ocypete* on it. Evidence that *junia* is host-specific comes from oviposition tests on a single captive adult, plus the finding of

11 eggs (eggs are laid singly and independently in this species) on plant 14. Our evidence for categorizing *erichto* is less firm, and consists only of oviposition trials on three captive adults. All were tested on plants 1 through 18 with the exception of Nos. 3 and 4. No acceptances of any species other than No. 15 were recorded, and we obtained 16 such acceptances.

For two of the three species classified as specialists, *arnaea* and *junia*, data obtained from the field are concordant with those obtained from captive or semi-captive insects. This concordance between field and lab data reassures us that our laboratory data do seem to have meaning. The third specialist, *erichto*, was classified from behavior of captive adults and larvae. Three adult *erichto* that were preference-tested would accept only an epiphytic sedge that hung from trees (16 acceptances observed), and the larvae likewise refused to feed on plants other than this sedge.

Among those insects classified as generalists, we have adequate field data for *myncea*, *hesione*, *libye*, *renata*, *hermes*, *themis* and *penelope* (although *themis* was rare in our study sites, we obtained data from nearby populations of this insect). For *alcinöe* we were able to perform preference trials on both captive adults and larvae, but for *palladia* and *ocypete* our only data are from larval feeding preferences. For these two species, we regard our classification of diet breadth as extremely tentative.

RELATIONSHIPS BETWEEN INSECT AND PLANT TRAITS

The lack of significant correlation between rank orders of insect species richness and host species richness indicates the relatively minor role played by specialists and their hosts in our data set. The only significant trend is a positive correlation between insect abundance and host abundance (Table 3), and this appears only after "specialist removal". Even this is not a conspicuous trend. There are clear exceptions to it, as the example of site POS 2 shows. At this site, species 13 served as the sole host of nine butterfly species, even though it was rare (Table 1). Our results contrast with those obtained from heliconiine butterflies and *Passiflora*, which have shown correlations between species richness of the insects and that of their host plants (Gilbert & Smiley 1978).

EFFECTS OF HABITAT FRAGMENTATION

The concordance between the distribution of specialists and that of the habitats available to them indicates that, at least for this set of species, habitat fragmentation had not resulted in significant local extinction of these species at the time of our study (1970-74). The presence of any of the three monophagous species in a habitat could be confidently predicted from the presence of its host species. The data of Figure 1 show *erichto* and *junia* distributed among sites in precisely the same manner as their respective hosts, while *arnaea* was recorded from six of the seven sites where its host grew. This phenomenon was especially striking since

Table 3. Spearman correlation coefficients.

Correlation between:	Correlation coefficient		Significance of correlation	
	All Species	Generalists	All Species	Generalists
Butterfly/ plant species	0.426	0.514	0.110	0.064
Butterfly species/ plant abundance	0.290	0.356	0.208	0.157
Plant/ butterfly abundance	0.349	0.562	0.162	0.046
Plant species/ Butterfly abundance	0.393	0.474	0.131	0.084

junia was absent from POS 1 and POS 3, which were both only about 50 m from POS 2 where *junia* and its host were common.

There was no trend in our data for the more isolated habitat patches (POS, Dump and Guanapo) to contain fewer species. However, much larger sample sizes would be needed for such a test to have sufficient power.

On a larger scale, we found no evidence for loss of species from the island of Trinidad. We recorded fifteen species, while Barcant (1970) lists seventeen satyrines recorded from Trinidad since lepidopterists first collected there in the 1890's. One of these seventeen (*calpurnia*) was recorded from a single site only, in 1932, while a second (*brixiola*) had been recorded only twice. We did not find either of these very rare species. Although Barcant recorded *palladia* as present in Trinidad, he was describing misidentified *myncea* (Singer et al 1983). *Palladia* does, indeed, occur there, but was apparently not found by Barcant (1970) or by other butterfly collectors.

Although human activities must have removed many formerly suitable habitats for these insects, at the time of this study they had not yet resulted either in extinction of species from Trinidad, or in significant reduction of the ability of host specialists to maintain populations in patches of habitat where their hosts still occurred.

Summary

Eleven species of Trinidadian satyrine butterflies were found to be generalist feeders as larvae, while three were monophagous. The presence of a monophagous satyrine at a site was accurately predicted from the presence of its host. This relationship, coupled with a comparison of our data with historical records, shows that, at the time of our study (1970-74), habitat fragmentation had not resulted in significant loss of

these insects either from local habitats suitable for them or from the Island of Trinidad as a whole.

Comparison between sites showed no significant correlation between insect species richness or abundance and host plant species richness or abundance. If generalist feeders and their hosts were considered separately, they showed a significant relationship between insect abundance and plant abundance. This trend, however, was not a very clear one, and there were striking exceptions to it. There was considerable overlap in resource utilization, with nine insect species using the same host species at one of our study sites.

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