A *HELICONIA* INSECT COMMUNITY IN A
VENEZUELAN CLOUD FOREST[1]

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Abstract. An experimental study was designed to evaluate the importance of first-order species interactions, higher-order species interactions and habitat (flower bract) age on the survivorship of 4 species of insects living in the water-filled floral bracts of *Heliconia bihai* L. in a Venezuelan cloud forest. Only 3 out of 16 first-order species interactions were statistically significant and they included both competitive and symbiotic effects. A higher-order effect was found for only 1 of 4 species while habitat age was found to influence 3 of 4 species. The experimental results indicate that for 3 species survival is greater in the older habitats. These results correspond to data from field studies on non-experimental inflorescences in which insects were found most frequently in mature floral bracts.

The results of this study are similar to those of an earlier study (Seifert and Seifert 1976*a*) on 2 species of *Heliconia* from lowland Costa Rica. We propose that *Heliconia* insect communities in general show low levels of 1st-order species interactions, some of which are symbiotic, and that higher-order species interactions are not a general component of these communities.

Key words: competition; first-order species interactions; habitat age effects; Heliconia; *higher-order species interactions; insects; symbiosis; Venezuela.*

INTRODUCTION

A major objective of community ecology is to detect the dynamic factors which determine the relative abundances and distributions of species in communities and to determine if recurring, predictable patterns exist. Some patterns have been shown to exist in similar communities at different locations. For example, Pianka (1967, 1969, 1971) has shown how a complex of factors including climate, vegetational structure and competition correlate with the number of coexisting lizard species in North America, Australian and African deserts. However, it may prove difficult to make generalizations about communities of taxonomically different organisms. While Paine (1966, 1971) found that predation determined species richness of intertidal invertebrate communities, Addicott (1974), who studied invertebrates living in pitcher plant pitchers, found that this pattern could not be generalized to all predator-prey communities. Some studies of populations and communities throw doubt on the ability to make general statements about community dynamics. Brockelman (1969), studying American toad tadpoles, and Ehrlich et al. (1975), studying checkerspot butterfly populations, showed that these populations could be regulated by different factors under similar environmental conditions.

In this report we discuss the community of insects living in the water-filled floral bracts of a plant, *Heliconia bihai* L. (Musaceae), located in a mid-elevation Venezuelan cloud forest. Our study was a test for the recurrence of similar dynamic factors in structuring taxonomically related Neotropical insect communities from different locations. We designed experiments to estimate the effects of interactions among these insects and compared the results with those previously obtained from the communities of insects in the inflorescences of 2 lowland Costa Rican *Heliconia* species (Seifert and Seifert 1976*a*). We attempted to maximize the probability of finding different results between these studies by using *Heliconia* species at different elevations. The *Heliconia* insect communities in Costa Rica and Venezuela were exposed to different temperature and humidity regimes. Our design also tested the importance of higher-order interactions in the *H. bihai* insect community: that is, interactions among 4 species systems which could not be predicted from results of 2 species systems. Further, we considered the importance of habitat age by determining the mortality rates of 4 species of insects living in *Heliconia* floral bracts of different ages.

MATERIAL AND METHODS

Our research was carried out within 4 km of Estación Biológica Rancho Grande, Parque Nacional Henri Pittier, Aragua, Venezuela (10°21′N, 65°41′W; Fleming 1947) at elevations ranging from 1000 to 1200

m. Rancho Grande is in an area of primary tropical premontane wet forest (Ewel and Madriz 1968), commonly characterized as a cloud forest (Beebe and Crane 1947). The area has a dry season from December through May. Clouds cover the forest during the late afternoons of the dry season, although rain seldom falls then. *Heliconia bihai* is the only *Heliconia* species at Rancho Grande with large erect bracts which blooms during the dry season. (*Heliconia* identifications follow Aristeguita [1961] who lists the genus in the family Musaceae. Other workers place *Heliconia* in a family of its own, the Heliconiaceae [Tomlinson 1969]. Our *H. bihai* is not the same species as that studied by Maguire et al. [1968] in Puerto Rico. By their photograph, the Puerto Rican species is *H. caribaea* Lamarck.) A mature inflorescence may have up to 9, alternately arranged narrow (about 4 cm), long (up to 15 cm) bracts each of which contain small amounts of water. The floral bracts mature sequentially. The top most bract is the youngest and each successively lower bract is about a week older than the one above it.

The bracts of *Heliconia bihai* contain a community of semiaquatic insects which are dominated numerically by larvae of *Quichuana angustriventris* (Macquart) (Diptera: Syrphidae) (= *Q. picadoi* Knab in Seifert and Seifert 1976a and *Q. aurata* Welker in Seifert and Seifert 1976b), *Copestylum roraima* (Curran) (Diptera: Syrphidae) and *Cephaloleia neglecta* Weise (Coleoptera: Chrysomelidae) and adults of *Gillisius* sp. #3 (Coleoptera: Hydrophilidae) (the 3rd undescribed species of *Gillisius* from our studies). The feeding habits, mobility and developmental times of these insects differ slightly. *Quichuana angustriventris* feeds primarily on detritus and floral parts and less commonly is found within the flower feeding on nectar. The larval development of *Q. angustriventris* takes about 45 days. While *Copestylum roraima* feeds on the same food sources as *Q. angustriventris*, *C. roraima* is found more commonly inside the flower feeding on nectar than is *Q. angustriventris*. The larval development time of *C. roraima* is about 50 days. Both of these syrphid larvae live below the water line within the bract but move occasionally from bract to bract on the same inflorescence. *Cephaloleia neglecta* has the most divergent feeding behavior and feeds by rasping the inside of the bract along the edge of the water line. *Cephaloleia neglecta* larvae, which have a larval life stage of about 32 days, move to younger bracts on the inflorescence as the bracts mature and rarely may move to an inflorescence on a 2nd plant (Seifert and Seifert, in press). *Gillisius* sp. #3 feeds on flower parts, the surface of the inside of the bract, and detritus and does so by crawling down the inside of the bracts and into the water. *Gillisius* sp. #3 is the most vagile of the 4 insect species and moves easily among bracts and inflorescences. Detailed information on the life histories of taxonomically related

TABLE 1. Number of inflorescences and initial densities of insects used in manipulation experiments. Top and left margins represent insect densities, cell entries are the number of inflorescences (consisting of 4 bracts) in each treatment.

| | | Quichuana | | | | | | | | |
| | | 0 Gillisius | | | 5 Gillisius | | | 10 Gillisius | | |
Cope-stylum	Cepha-loleia	0	5	10	0	5	10	0	5	10
10	10	2	...	...	...	...	1	...	...	2
	5	2	...	...	...	1	...	...	...	...
	0	1	1	3	2	...	...	2	...	...
5	10	1	...	...	...	1	...	...	...	...
	5	1	...	...	...	2	1	...	1	...
	0	2	2	1	2	...	...	1	...	...
0	10	1	1	2	1	...	...	2	...	2
	5	1	2	1	2	...	...	1	...	...
	0	...	1	1	2	2	1	1	2	2

species in Costa Rica have been published elsewhere (Seifert and Seifert 1976b).

From February through June 1976 we ran experiments to determine the effects of 1st-order species interactions, the effects of higher-order interactions and the effects of bract age on the insects living in *H. bihai* inflorescences. During the *H. bihai* flowering season, young, emergent buds were located and enclosed in plastic bags tied securely at the rachis. These bags prevented insect oviposition and immigration and insured that the buds would become inflorescences without insects. There was no evidence that the bagging technique itself had any effect on bract development: bagged and unbagged bracts grew at the same rates and accumulated similar amounts of water. Buds were allowed to grow in the bags until they reached a size of 4 bracts (ages from 4 to 6 weeks). At this time the bags were removed and varying densities of 1, 2 or all 4 insect species were added to each bract. (Three species experiments were not run due to limitations of time and inflorescence availability.) Table 1 lists the treatments run and the number of inflorescences used in the experiments. The experimental densities used per bract included densities higher than the mean densities found in the wild (see Table 2). After manipulation, a small plastic bag was tied around the top (as yet unopened) bracts so that no additional food beyond that in the manipulated bracts would be available. Once the experiments began, no attempt was made to reduce immigration from other inflorescences into the experimental bracts. The experiments ran for 6, 7 or 8 days after which the inflorescences were cut and each bract was put into a separate plastic bag, returned to the field station and dissected. The number of each insect species remaining in each bract was recorded.

For each of the 4 species we analyzed the results of the experiments using a multiple linear regression analysis of the form

TABLE 2. Cumulative frequency distributions of 4 species of insects in the youngest (top) 4 bracts of nonmanipulated *Heliconia bihai* inflorescences.

Insect species, Cumulative frequency and D	Total number of individuals	Bract number (age)			
		1 (youngest)	2	3	4 (oldest)
Quichuana	34				
Cumulative frequency		0.0	0.059	0.882	1.00
D			0.441***		
Gillisius	25				
Cumulative frequency		0.0	0.280	0.400	1.00
D				0.350**	
Copestylum	325				
Cumulative frequency		0.025	0.295	0.735	1.00
D		0.225***			
Cephaloleia	128				
Cumulative frequency		0.180	0.562	0.836	1.00
D				0.086 ns	

NOTE: Forty-eight inflorescences were allocated randomly among 4 groups; the data for each insect species come from 12 inflorescences. The differences between even distributions over bracts and the observed insect distributions are tested for each species by the Kolmogorov-Smirnov one-sample test, the test statistic of which, D, is given for each species. For a 4 way group comparison at an overall probability level of $P \leq .05$, individual comparisons must be significant at $P \leq .017$. Statistical significance is indicated as follows: ns = $P > .10$, ** = $.005 > P > .001$, *** = $P < .001$.

$$(1/N_w)(dN_w/dt) = a_0 + a_{ww}N_w + \sum_{x=1}^{z} a_{wx}N_x$$
$$+ a_{wxyz}(N_x N_y N_z)/(1000) + a_{wB}B,$$
$$x \neq w. \quad (1)$$

In equation (1) the dependent variable is the per capita change in the numbers of species w with respect to time (a mortality rate), N_w through N_z are the initial densities of each of the 4 insect species and B is the bract number (1 through 4, with bract 1 representing the youngest bract) in which the experiment took place. The independent variable which represents the higher-order effect $(N_x N_y N_z)/(1000)$, is the product of the initial values of all species (except that represented by the dependent variable) divided by 1000. The division by 1000 is a scaling procedure which reduces the computer error associated with the large values of $(N_x N_y N_z)$. Five experimental bracts were identified as outliers by a gap test and were removed before the multiple linear regressions were run. The generated partial regression coefficient a_{ww} is interpretable as the effect of species w on itself, a_{wx} is the effect of species x on species w, a_{wxyz} is the higher-order effect of species x, y and z on species w and a_{wB} is the bract (habitat age) effect. These effects reflect differences in insect survival within the inflorescence but cannot reflect any changes in developmental times or fecundity rates. When a significant bract effect was found, the interactions in each bract were tested separately using an *a posteriori* multiple linear regression.

During the course of the *H. bihai* flowering season we collected 48 nonmanipulated wild inflorescences of 4 bracts or greater and recorded the number of individuals of each insect species in each of the top

(youngest) 4 bracts. These represent bracts of the same ages as those used in the experiments. The inflorescences were allocated randomly among 4 groups, 1 group for each insect species. The random allocation of inflorescences gave us independent estimates of the natural densities of each insect species as well as their distributions over bracts. Four Kolmogorov-Smirnov 1-sample tests were run to test the null hypotheses that each insect species was distributed evenly over bracts. Each independent Kolmogorov-Smirnov test was tested at $P \leq .017$ in order to give an overall significance level of $P \leq .05$. The results of these tests then were compared with the estimations of bract effects from the experimental analyses.

RESULTS

All regression equations that included 1st-order species interactions, higher-order species interactions and bract effects were statistically significant at $P \leq .025$, however, only 7 of the 24 partial regression coefficients associated with these equations were significant at $P \leq .05$ (Table 3). (The raw data for each bract are available on request.) Three 1st-order species interaction coefficients were significant. These include an intraspecific competitive effect of *Cephaloleia neglecta*, an interspecific competitive effect of *Copestylum roraima* on *Cephaloleia neglecta* and a generalized symbiotic (facultatively commensal) effect of *Cephaloleia neglecta* on *Gillisius* sp. #3. The competitive effect of *Copestylum roraima* on *Cephaloleia neglecta* is difficult to interpret since the 2 species have distinct feeding habits. We have seen feeding *Cephaloleia neglecta* larvae leave a bract because of disturbance by syrphid larvae, and increased numbers of *Copestylum roraima* larvae would cause more dis-

TABLE 3. *F* ratios and probability levels for partial regression coefficients plus all statistically significant coefficients for each of 4 multiple linear regression equations.

Dependent variable	Independent variables					
	Q	*G*	*Cope*	*Ceph*	*H-O*	*Bracts*
Quichuana						
F ratio	1.64 ns	0.13 ns	0.11	0.23 ns	0.23 ns	16.06***
Significant partial regression coefficients						0.0156
Gillisius						
F ratio	1.96 ns	0.48 ns	0.97 ns	12.62***	4.48*	4.20*
Significant partial regression coefficients				0.0077	−0.0052	0.0114
Copestylum						
F ratio	1.86 ns	2.23 ns	2.12 ns	0.30 ns	0.56 ns	23.30***
Significant partial regression coefficients						0.0190
Cephaloleia						
F ratio	0.44 ns	2.08 ns	5.50*	9.05**	1.29 ns	0.32 ns
Significant partial regression coefficients			−0.0040	−0.0065		

NOTE: The terms *Q, G, Cope, Ceph* and *H-O* stand for *Quichuana, Gillisius, Copestylum, Cephaloleia* and higher-order effect, respectively. Statistical significance is indicated as follows: ns = $P > .05$, * = $.05 > P > .01$, ** = $.005 > P > .001$, *** = $P < .001$.

turbance of *Cephaloleia neglecta* larvae. It is not clear why a similar effect did not occur due to the presence of *Quichuana angustriventris* larvae. The symbiotic effect of *Cephaloleia neglecta* on *Gillisius* sp. #3 was due to the increase in detritus levels and a change in the kinds of food available caused by the shredding of the bract as *Cephaloleia neglecta* larvae fed. *Gillisius* sp. #3 may have responded more intensely to the feeding behavior of *Cephaloleia neglecta* than did the syrphid larvae since *Gillisius* sp. #3 feeds part of the time directly on the bract, on microorganisms and damaged plant material.

Only in the case of *Gillisius* sp. #3 was the partial regression coefficient for higher-order interactions statistically significant, indicating that the joint occurrence of *Q. angustriventris, Copestylum roraima* and *Cephaloleia neglecta* had a significant competitive effect on *Gillisius* sp. #3 while each species alone did not.

Bract effects, which reflect different habitat ages, were significant and positive for 3 of the 4 regression equations. For *Q. angustriventris, Gillisius* sp. #3 and *C. roraima* the mortality rates were lower in the older bracts. For *C. neglecta*, no bract effect was demonstrated: survivorship was about equal in each of the youngest 4 bracts. These experimental results agreed with the results of the Kolmogorov-Smirnov tests on insect distributions over bracts in the natural (non-manipulated) populations. The Kolmogorov-Smirnov tests showed a significant deviation from an even distribution over the bracts for *Q. angustriventris, Gillisius* sp. #3 and *C. roraima* (Table 2): insect species which were found most frequently in the lower, more mature bracts.

Bract by bract *a posteriori* multiple linear regressions were run for each of the 3 species showing significant bract effects. In all cases, the regression equations were not statistically significant at $P \le .05$.

DISCUSSION

The results of these experiments reveal that general patterns do exist in *Heliconia* insect communities. Through experimentation on mid-elevation Venezuelan *Heliconia* insect communities we have found low levels of species interactions and the presence of symbiotic effects. These results concur with our previous work on 2 lowland Costa Rican *Heliconia* insect communities which consisted of insect species congeneric with those found in Venezuela (Seifert and Seifert 1976a). Similarities exist even though the communities were about 2000 km apart, 1000 m different in elevation and exposed to different climates. The Costa Rican and Venezuelan *Heliconia* insect communities studied showed low levels of both intraspecific and interspecific competitive effects with some symbiotic species interactions (Seifert and Seifert 1976a). In the Venezuelan *H. bihai* community only *Cephaloleia neglecta* showed intraspecific competition. At Rancho Grande these beetles often strip the entire surface off the bracts (Seifert and Seifert, *in press*) indicating that resource limitation commonly occurs. This is in contrast with *Cephaloleia puncticollis* Baly from Costa Rica which feeds on, but does not deplete, the bract resource (Seifert and Seifert 1976a) and with other beetles in the same subfamily which feed on, but do not completely consume, *Heliconia* leaves in Central America (Strong 1977) and Venezuela (Seifert and Sei-

fert, *in press*). The remaining insect species in *H. bihai* did not show intraspecific competitive effects at the experimental densities. Since the experimental densities were chosen to be equal to or > natural densities, intraspecific competition, based on survival in the floral bracts, cannot be demonstrated to be an important controlling factor of these 3 insect populations.

We have experimentally demonstrated that low levels of interspecific competition occur among insects in *Heliconia bihai* inflorescences. While the varied feeding habits among the insects indicate that interspecific competition is reduced due to resource partitioning, the demonstration of low levels of intraspecific competition implies that the lack of interspecific competition among these insects is primarily due to low population levels in the bracts. Low bract population levels may be due to adult females rejecting previously occupied bracts as oviposition sites, as has been shown to occur for *Q. angustriventris* in Costa Rica (Seifert and Seifert 1976*b*). Alternatively, adult mortality without replacement during times when *Heliconia* plants are not blooming may lead to low levels of oviposition and subsequent low levels of larvae in the bracts (Seifert and Seifert 1976*a,b*). At Rancho Grande, there is a period of about 2 months before the *H. bihai* blooming season when no species of *Heliconia* are blooming. During this time, reproduction and population growth for *Q. angustriventris, Copestylum roraima* and *Cephaloleia neglecta* does not occur.

Both *Cephaloleia neglecta* from Venezuela and the related *C. puncticollis,* whose larvae feed on the bracts of *H. imbricata* (Kuntze) Baker in Costa Rica, act as symbionts in the *Heliconia* insect community. These beetles destroy the inside bract surface and increase the food source for some of the other insects. We predict that *Cephaloleia* larvae in other *Heliconia* insect communities also will act as symbionts. Hodkinson (1975) recognized a corresponding functional feeding group, shredders, in aquatic insect communities in beaver ponds. Shredders reduced the size of organic particles and made them available for detritus feeding insects, thus acting as generalized symbionts.

We found that higher-order interactions were only important for 1 of the insect species, *Gillisius* sp. #3, and in this species only a 1st-order symbiotic effect was statistically significant. These results are again in agreement with our previous findings. *A posteriori* tests of Costa Rican *Heliconia* insect communities did not show higher-order effects (Seifert and Seifert 1976*a*). Only the Venezuelan field research, however, was designed to test specifically for the presence of higher-order effects. Vandermeer (1969) found similar results when studying 4 competing species of protozoans in the laboratory. There, in only 1 of 4 cases were higher-order interactions significant and Vandermeer concluded that, on a community level, higher-order interactions were not important. Likewise,

Richmond et al. (1975) found that the results of the interactions among 3 species of *Drosophila* in laboratory cultures could be predicted on the basis of results from 2 species experiments. Our results are different from studies by Wilbur (1972) on a 6 species amphibian community and by Neill (1974) on a 4 species crustacean community both of which displayed significant higher-order interactions. Our data do not support the suggestion of both of these authors that higher-order interactions are general attributes of natural communities. Clearly, these different taxa have different community structuring factors.

Finally, we document that habitat age, as estimated by bract age, is important in determining the survival rate of insects living in the inflorescences. Increased densities and survivorship are associated with older bracts for 3 of the 4 insect species. The experimental and observational results are in agreement: the species that showed an experimental bract effect are also the species that had uneven distributions over nonexperimental bracts. Bracts are not uniform in their ability to provide food. More mature flowers and bracts increase the food quality for 3 of the insect species. Such differential food quality could involve changes in microorganism composition or differences in kinds of detritus. More importantly for the fly species, older bracts include blooming flowers which produce nectar; the flowers in the youngest bracts have not begun nectar production yet. Notice that the experimental results, which did not indicate density dependent mortality due to intraspecific competition, imply that the bract effect is not due simply to increases in the quantity of food available. Food quantity changes would have been reflected by increased mortality as experimental densities increased in each bract. Only in the case of the bract eating beetle larva, *Cephaloleia neglecta,* was a nonsignificant bract age effect shown. Apparently, all of the bracts studied were young enough to be easily fed upon by beetle larvae. While bract effects are important in Venezuelan *H. bihai* insect communities, a statement about the generality of these effects must be tempered by the recognition that we do not have data to indicate the importance of bract effects in Costa Rican *Heliconia* communities.

These bract age effects in *H. bihai* can be considered in relation to general effects of different aged habitats on arthropods. Some other temporary habitats, such as dung pats and fallen logs, have arthropod successions with distinct seral stages (Mohr 1943, Fager 1968). In such communities species replacements occur as the habitats become older. In this study of *Heliconia* insect communities changes in survival rates and abundances occurred as the habitats aged but we did not evaluate experimentally changes in insect species composition over the lives of the inflorescences. Our field observations on the insect com-

munity in *H. bihai* inflorescences indicate that different aged habitats have similar species compositions except that habitats older than those studied experimentally have few *C. neglecta* larvae (Seifert and Seifert, *in press*) and the oldest habitats are completely devoid of the fly and beetle species associated with the semi-aquatic habitats. The oldest habitats are rotting flower parts without any standing water and are inhabited by a terrestrial group of decomposers such as mites and collembola.

In summary, the results of investigations on *Heliconia* insect communities show the importance of habitat (bract) age effects and indicate general recurring patterns of low levels of 1st-order competitive effects, some symbiotic effects and a lack of higher-order interactions. Low levels of competition due to resource partitioning and the presence of symbiotic interactions such as those found in *Heliconia* insect communities may be more common features of tropical environments than of temperate environments (Futuyma 1973). In *Heliconia* insect communities low levels of competition are primarily the result of low population levels.

LITERATURE CITED

Addicott, J. F. 1974. Predation and prey community structure: an experimental study of the effect of mosquito larvae on the protozoan communities of pitcher plants. Ecology 55:475–492.

Aristeguieta, L. 1961. El genero *Heliconia* en Venezuela. Instituto Botanico, Dirección de Recursos Naturales Renovables, Ministerio de Agricultura y Cría, Caracas, Venezuela.

Beebe, W., and J. Crane. 1947. Ecology of Rancho Grande. Zoologica 32:43–60.

Brockelman, W. Y. 1969. An analysis of density effects and predation in *Bufo americanus* tadpoles. Ecology 50:632–644.

Ehrlich, P. R., R. R. White, M. C. Singer, S. W. McKechie and L. E. Gilbert. 1975. Checkerspot butterflies: a historical perspective. Science 188:221–228.

Ewel, J. J., and A. Madriz. 1968. Zonas de vida de Venezuela. Dirección de Investigación, Ministerio de Agricultura y Cría, Caracas, Venezuela.

Fager, E. W. 1968. The community of invertebrates in decaying oak wood. Journal of Animal Ecology 37:121–142.

Fleming, H. 1947. Sphingidae (moths) of Rancho Grande, north central Venezuela. Zoologica 32:133–145.

Futuyma, D. J. 1973. Community structure and stability in constant environments. American Naturalist 107:443–445.

Hodkinson, I. D. 1975. A community analysis of the benthic insect fauna of an abandoned beaver pond. Journal of Animal Ecology 44:533–551.

Maguire, B., Jr., D. Belk, and G. Wells. 1968. Control of community structure by mosquito larvae. Ecology 49:207–210.

Mohr, C. O. 1943. Cattle droppings as ecological units. Ecological Monographs 13:275–298.

Neill, W. E. 1974. The community matrix and interdependence of the competition coefficients. American Naturalist 108:399–408.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist 100:65–75.

———. 1971. A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. Ecology 52:1096–1106.

Pianka, E. R. 1967. On lizard species diversity: North American flatland deserts. Ecology 48:333–351.

———. 1969. Habitat specificity, speciation, and species density in Australian desert lizards. Ecology 50:498–502.

———. 1971. Lizard species density in the Kalahari desert. Ecology 52:1024–1029.

Richmond, R. C., M. E. Gilpin, S. Perez Salas and F. J. Ayala. 1975. A search for emergent competitive phenomena: the dynamics of multispecies *Drosophila* systems. Ecology 56:709–714.

Seifert, R. P. and F. H. Seifert. 1976*a*. A community matrix analysis of *Heliconia* insect communities. American Naturalist 110:461–483.

———. 1976*b*. Natural history of insects living in inflorescences of two species of *Heliconia*. Journal of the New York Entomological Society 84:233–242.

———. *In press*. Utilization of *Heliconia* (Musaceae) by the beetle *Xenarescus monocerus* (Oliver) (Chrysomelidae: Hispinae) in a Venezuelan forest. Biotropica.

Strong, D. R., Jr. 1977. Rolled leaf hispine beetles and their Zingiberales host plants in Middle America. Biotropica 9:156–169.

Tomlinson, P. B. 1969. Anatomy of the monocotyledons. III. Commelinales-Zingiberales. The Clarendon Press, Oxford, England.

Vandermeer, J. H. 1969. The competitive structure of communities: an experimental approach with protozoa. Ecology 50:362–371.

Wilbur, H. M. 1972. Competition, predation, and the structure of the *Ambystoma–Rana sylvatica* community. Ecology 53:3–21.