

ECOLOGICAL PATTERNS OF AQUATIC INSECT COMMUNITIES IN TWO *HELIAMPHORA* PITCHER-PLANT SPECIES OF THE VENEZUELAN HIGHLANDS

PATRONES ECOLOGICOS DE LAS COMUNIDADES DE INSECTOS ACUATICOS DE DOS ESPECIES DE PLANTAS HELIAMPHORA DE LAS ALTIPLANICIES VENEZOLANAS

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ABSTRACT

This paper compares the insect community of two neotropical insectivorous pitcher-plants (*Heliamphora nutans*, *H. heterodoxa*) of the Highlands of Guayana, Venezuela, in the dry and wet seasons, and compares them with analogous nearctic pitcher-plants. Each *Heliamphora* species harbored a mosquito and a midge species. Patterns of insect micro-distribution among leaves, and specific adaptations of mosquitoes (*Wyeomyia zinzala*, *W. fishi*) such as concentrated oviposition in the youngest leaves resembled those of the nearctic *Sarracenia purpurea* (*W. smithii*). Insect abundance was related to leaf size (large > small), age (young > old), and climate (wet > dry season). In both *Heliamphora* species, the relative abundance of mosquitoes and midges was the same but changed during the dry season when mosquito but not midge abundance declined. Mosquito and midge densities were positively correlated in the wet season and negatively in the dry season when their distributions separated by leaf age. Each *Heliamphora* species, containing only two insect species, appeared poorer in species than *S. purpurea* which also harbors sarcophagids, but richer than *D. californica* which hosts only one species. *H. nutans* and *H. heterodoxa* insect communities do not follow the tendency of increased biotic diversity with decreasing latitude.

KEY WORDS: communities, aquatic insects, phytotelmata, *Heliamphora*, *Sarracenia*, *Wyeomyia*, latitudinal comparison.

RESUMEN

El objetivo fue describir la comunidad de insectos de dos plantas insectívoras (*Heliampora nutans*, *H. heterodoxa*) de Guayana, Venezuela, en las épocas húmedas y secas, y compararlas con sus equivalentes neárticas. Las especies de *Heliampora* alojaban una especie de mosquito y de quironómido. Los patrones de micro-distribución de insectos entre hojas, y adaptaciones específicas de los mosquitos (*Wyeomyia zinzala*, *W. fishi*) como la oviposición concentrada en las hojas más jóvenes, fueron similares a las existentes en *Sarracenia purpurea* (*W. smithii*) del neártico. La abundancia de insectos varió con el tamaño de la hoja (grande > pequeña), edad (joven > vieja), y clima (estación húmeda > seca). En ambas especies de *Heliampora* existieron proporciones similares de mosquitos a quironómidos, pero en la época seca la densidad de mosquitos se redujo a la mitad. Las densidades de mosquitos y quironómidos resultaron correlacionadas positivamente en la época húmeda y negativamente en la época seca, cuando sus distribuciones aparecieron separadas por edad de las hojas. Las especies de *Heliampora* resultaron ser más pobres en especies que *S. purpurea*, la que además contiene sarcófágidos, y más ricas en especies que *D. californica* que posee solo una especie. Las comunidades de insectos acuáticos de *H. nutans* y *H. heterodoxa* no siguen la tendencia de una incrementada diversidad de especies a bajas latitudes.

PALABRAS CLAVES: comunidades, insectos acuáticos, phytotelmata, *Heliampora*, *Sarracenia*, *Wyeomyia*, comparación latitudinal.

INTRODUCTION

Aquatic habitats called phytotelmata (Varga 1928a,b; Kitching 1971; Maguire 1971; Fish 1983) include a fairly diverse group of small bodies of water retained in plants or parts of plants such as axils of bromeliads and aroids, bamboo internodes, fallen fruits and leaves, treeholes, pitcher-plants, etc. Most phytotelmata occur in the Tropics. In the Temperate zone they are restricted to insectivorous pitcher-plants and tree holes. Phytotelmata are inhabited by aquatic insects, mainly Diptera and Coleoptera, and most phytotelmata contain at least one species of mosquito (Culicidae) whose immature stages are usually numerically dominant (Fish 1983). Leaves of insectivorous pitcher plants are modified to form a hollow tube that fills with water from plant secretions and/or rainfall, and act as traps for terrestrial arthropods (Lloyd

1942). Nearctic and neotropical pitcher plants live in swampy, savanna-like habitats probably poor in nutrients (Plummer 1963). Pitcher plants and associated insects rely upon captured prey arthropods to provide nitrogen and other essential elements for growth and reproduction.

New World pitcher-plants (*Sarraceniaceae*) belong to two nearctic genera (*Sarracenia* and *Darlingtonia*) and one neotropical genus (*Heliampora*). *Sarracenia* includes eight species most of which occur on the coastal plains of the southeastern United States, with *S. purpurea* extending northward to Labrador and Manitoba, Canada (McDaniel 1971). *Darlingtonia* is a monospecific genus, with *D. californica* occurring in northern California and southern Oregon (Lloyd 1942). Neotropical *Heliampora* comprises six species found only in the ancient

Highlands of Guayana, northern South America (Maguire et al. 1978).

Nearctic pitcher-plants sustain an endemic fauna of insects with aquatic stages, including mosquitoes, midges, and flesh flies (Jones 1935). The aquatic fauna of neotropical pitcher-plants had not been investigated before, and it was expected to include new species of mosquitoes and other aquatic insects. Of considerable biogeographical interest was to determine if *Heliamphora* insects were systematically related to those of *Darlingtonia* and *Sarracenia*.

Maguire et al. (1978) suggested that the Sarraceniaceae are neotropical in origin and that *Heliamphora* is the closest ancestral prototype of the three genera. The taxonomic relationships of nearctic and neotropical insects in pitcher-plants may parallel that of their host plants since the only mosquito (*Wyeomyia smithii*) living in nearctic pitcher-plants may be neotropical in origin (Ross 1964; Bradshaw and Lounibos 1977). If *W. smithii* is taxonomically closely related to the mosquitoes expected to be found in *Heliamphora*, it could indicate that the Sarraceniaceae once had a continuous distribution.

The presence of pitcher-plants in the nearctic and neotropical zones also provides the opportunity to compare aquatic communities living in equivalent micro-habitats at contrasting latitudes. Since biotic diversity is usually higher at lower latitudes, we expected to find more diverse communities living in *Heliamphora* than in *Sarracenia* or *Darlingtonia*.

The objectives of this research were to determine the composition, abundance and distribution of the aquatic insects living in two neotropical pitcher-plant species, and to compare them with the insect communities living in nearctic pitcher-plants.

STUDY AREA AND METHODS

We investigated *Heliamphora heterodoxa* at Km 146 of La Gran Sabana (5° 30' N, 61° 17' W; el.=1,400 m), Bolivar State, Venezuela, during the wet season (July) of 1982, and during the dry season (February) of 1983. Vegetation in this area was savanna-like with pitcher-plants living only in a large bog.

We investigated *H. nutans* at the summit of Mt. Roraima (5° 14' N, 60° 50' W; el.=2,700 m), Bolivar State, Venezuela, only during the wet season (July) of 1982. Vegetation at the summit is short and grows between the large blocks of bare sandstone, with pitcher-plants living in swampy areas.

Available mean annual temperature and mean total accumulated rainfall data from the nearest weather station were 21.6°C (1951-1960) and 1,649 mm (1940-1962) (Santa Elena de Uairen; 04° 36' N, 61° 07' W; el.= 910 m; Bolivar State, Venezuela; Ewel et al. 1976). Mean temperatures for February and July (same periods) are 21.8°C and 20.9°C. Mean accumulated rainfall for February and July (same periods) are 72 mm and 216 mm. There is a short dry season of three months from January to March, and a rainy season from May to August.

A total of 114 leaves from 20 plants of *H. heterodoxa* was sampled in the wet season, and 40 leaves from 16 plants in the dry season. A total of 83 leaves from 25 plants of *H. nutans* was sampled in the wet season only. For every plant, we examined the sequence in which leaves had opened and assigned to the most recently opened leaf the rank of one, the second the rank two, etc. The rank reflected the relative age of the leaf. This procedure allowed us to compare leaves of similar age in different plants regardless of the number of leaves a particular plant eventually developed. All leaves per plant were sampled for insects and all aquatic insects in each leaf were removed and counted. A subsample of insects was transferred alive to our laboratory for further biological observations. The remainder were preserved in 70 % Ethanol.

RESULTS

The pitcher plants

H. heterodoxa plants had larger, thicker leaves that held more water than the smaller *H. nutans*. Although water volume per leaf was not measured, we observed that the content of water in the leaves declined with their age in both *Heliophora* species. Rainy season *H. heterodoxa* had significantly more leaves per plant (t-test; $P < 0.01$) than *H. nutans*.

Figure 1 shows the rank-age distribution of leaves of *Heliophora*. Mean leaf rank was 4.1 (± 1.3 95% C.I.) for *H. heterodoxa* and 2.5 (± 0.5) for *H. nutans* in the rainy season. In both species, leaves older than rank 4

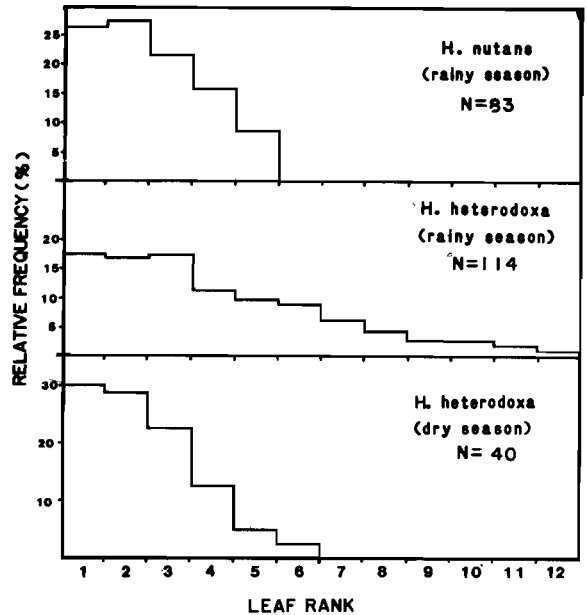


FIGURE 1. Relative frequency (%) of leaves of *H. nutans* and *H. heterodoxa* in different leaf ranks, and the number of leaves sampled in July 1982 (rainy season), and February 1983 (dry season).

generally exhibited senescence in the rainy season. The dissection of some unopened leaves of each species showed that they already contained water.

H. heterodoxa suffered reductions in the number of leaves with water during the dry season and had a mean leaf rank of 2.4 leaves per plant (± 0.7). The content of water of the leaves appeared to be reduced in comparison with the rainy season. The swamp with *H. heterodoxa* was drier in the dry season, and most of the leaves were senescent.

Community composition and insect abundance

The aquatic insect community inhabiting *H. nutans* was composed of a sabethinid mosquito described as *Wyeomyia zinzala* (Zavortink 1985, new

species), and an unidentified midge (Diptera: Chironomidae). A similar composition of aquatic insects was associated with *H. heterodoxa*. The mosquito was described as *Wyeomyia fishi* (Zavorlink 1985, new species) and is closely related to *Wyeomyia zinzala* from *H. nutans*. The midge found in *H. heterodoxa* could not be identified.

Mean abundance of mosquitoes (larvae/leaf) declined with the age of the leaf in both plant species and seasons (Fig. 2). Mosquito abundance was negatively correlated with leaf rank in

each plant species and for all seasons (overall $P < 0.001$). Changes in midge abundance with leaf rank were different for each plant and season (Fig. 2). Midge abundance was negatively correlated with leaf rank in *H. heterodoxa* during the rainy season ($r_s = -0.27$; $P < 0.005$) but positively correlated during the dry season ($r_s = 0.30$; $P < 0.025$). Midge abundance was not correlated with leaf rank in *H. nutans*.

Mosquito larvae were numerically dominant in relation to the midges in all plants and seasons (Fig. 2), except in the oldest leaves of *H. heterodoxa*. Mosquito abundance in *H. heterodoxa* decreased from 10.2 larvae per leaf (± 3.2 95% C.I.) in the rainy season to 5.7 (± 2.0) in the dry season. Mean mosquito abundance in *H. nutans* was 6.0 larvae per leaf (± 1.3) in the rainy season.

Mean midge abundance was 0.9 larvae per leaf (± 0.4) in *H. heterodoxa* in the rainy season, 1.2 (± 0.6) in the dry season, and 0.7 (± 0.2) in *H. nutans* during the rainy season.

Community structure

To examine the relative abundance of mosquitoes and midges at each leaf rank, we calculated the proportion of each species in each leaf rank (Fig. 3). The midges tended to be proportionately more common than mosquitoes in older leaves regardless of the plant species or the season.

The difference in medians of the mosquito-midge ratio per leaf was not significant ($P > 0.05$; Mann-Whitney test) between *H. nutans* ($5.0 \pm 3.5-7.5$) and *H. heterodoxa* ($5.5 \pm 3.5-9.2$) during the

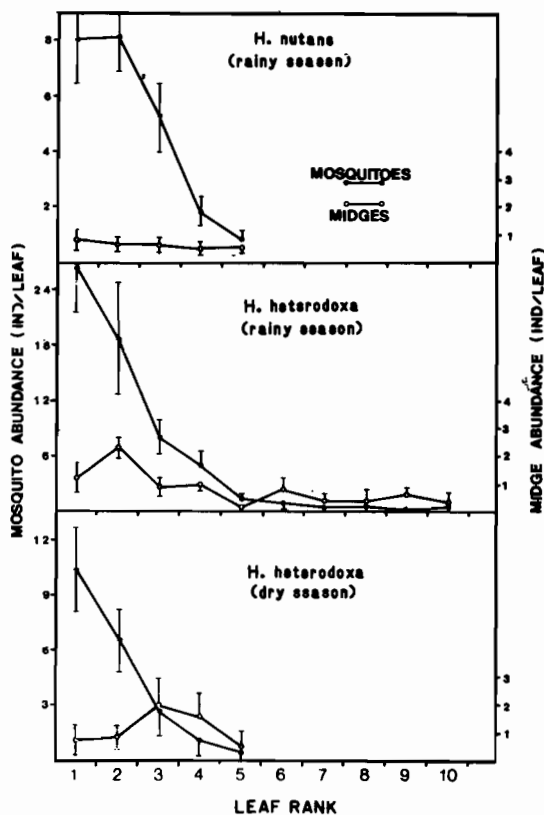


FIGURE 2. Mean abundance (individuals/leaf) and standard errors of immature stages of mosquito (*Wyeomyia* spp.) and midge species in different leaf ranks of *H. nutans* and *H. heterodoxa* collected in the rainy season (July, 1982), and the dry season (February, 1983).

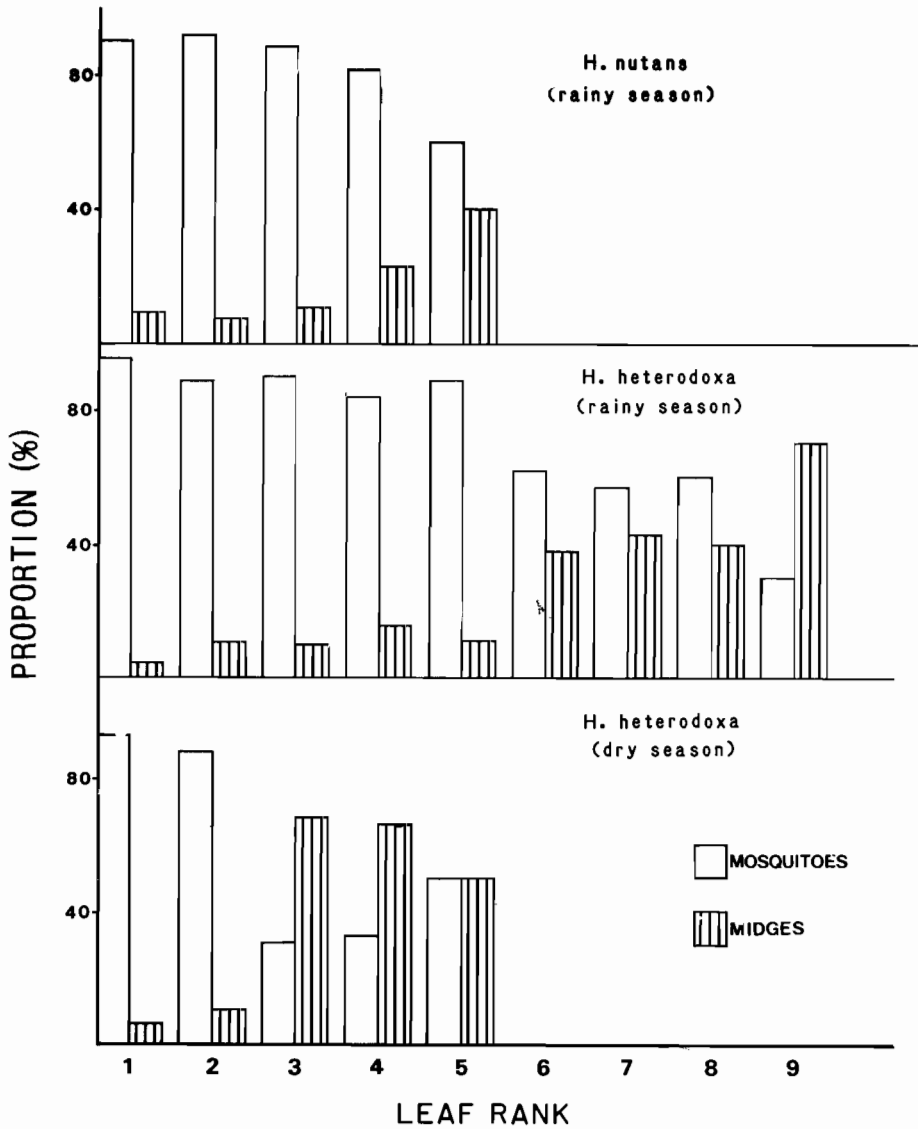


FIGURE 3. Proportion of immature mosquitoes and midges found in each set of leaves of given rank age, per pitcher plant species and season.

rainy season. The ratio mosquito-midge in *H. heterodoxa* was lower ($U=2120$; $P<0.025$) in the dry season than in the rainy season ($2.0 \pm 0.5-8.5$).

The numbers of mosquito and midge larvae were positively correlated in the leaves of *H. heterodoxa* during the

rainy season ($r_s=0.31$; $n=114$; $P<0.001$), but negatively associated during the dry season ($r_s=-0.33$; $n=40$; $P<0.02$). There was a positive, but non-significant correlation between mosquitoes and midges in the leaves of *H. nutans* during the rainy season ($r_s=0.20$; $n=83$; $P=0.067$).

Age structure

Mosquito eggs were observed concentrated on the internal walls of the youngest leaf of single plants of *H. nutans* and *H. heterodoxa*. Figure 4 shows

the distribution of first and second instars, third and fourth instars, and pupae of mosquitoes in the pitcher-plants. Early instars of mosquitoes were confined to early leaves of ranks one and two in *H. heterodoxa*. Mosquitoes in

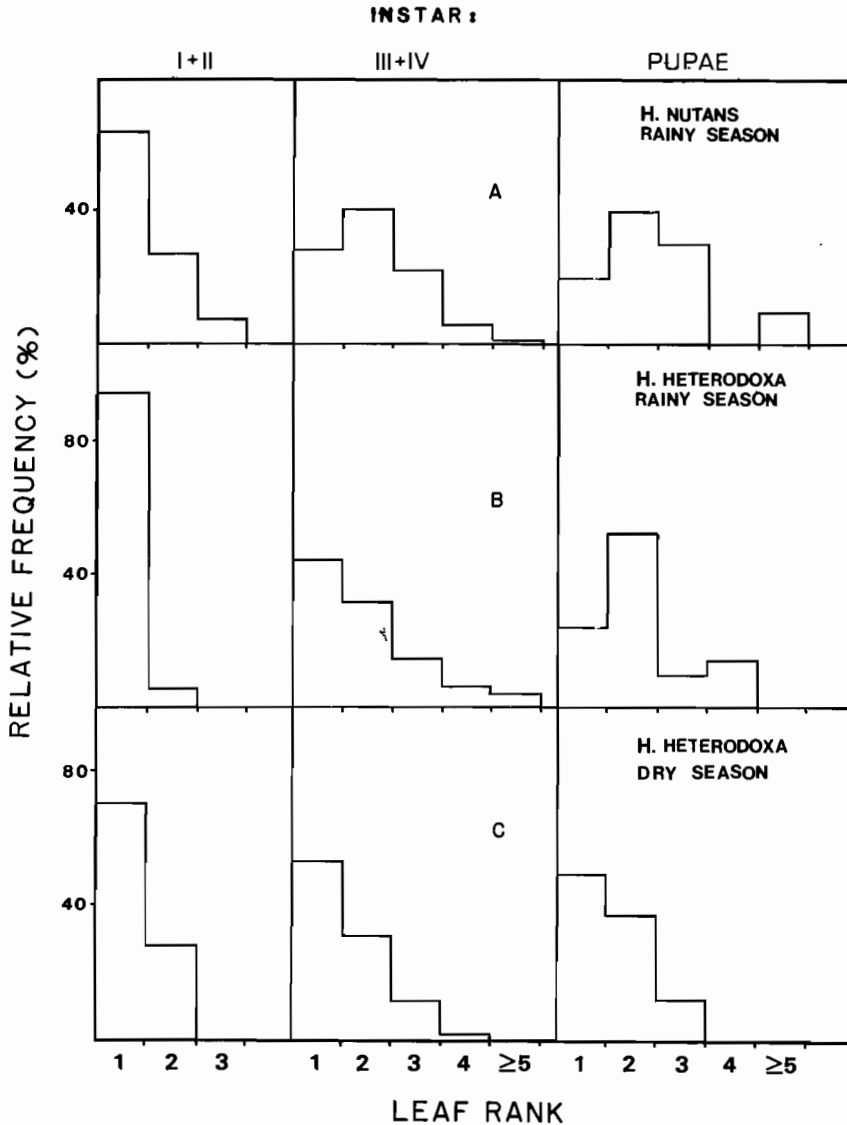


FIGURE 4. Relative frequency (%) of mosquitoes (*Wyeomyia* spp.) at given stages of preadult development in relation to host's leaf rank in: A) *H. nutans* (rainy season), B) *H. heterodoxa* (rainy season), and C) *H. heterodoxa* (dry season).

H. nutans exhibited a similar pattern of decreasing early instars with the leaf rank. Intermediate instars of mosquitoes tended to decrease in frequency with the age of the leaves in either pitcher plant or season (Fig. 4). Pupae of mosquitoes in the leaves of any pitcher-plant were recorded as early as in those of rank one.

Figure 5 shows the distribution of smaller and larger midge larvae and pupae among the leaves of the pitcher plants. It was not possible to identify the instars of the midges. Smaller midges were not confined to particular leaf ranks, but instead they were spread throughout leaves of different ages. Larger midges exhibited different

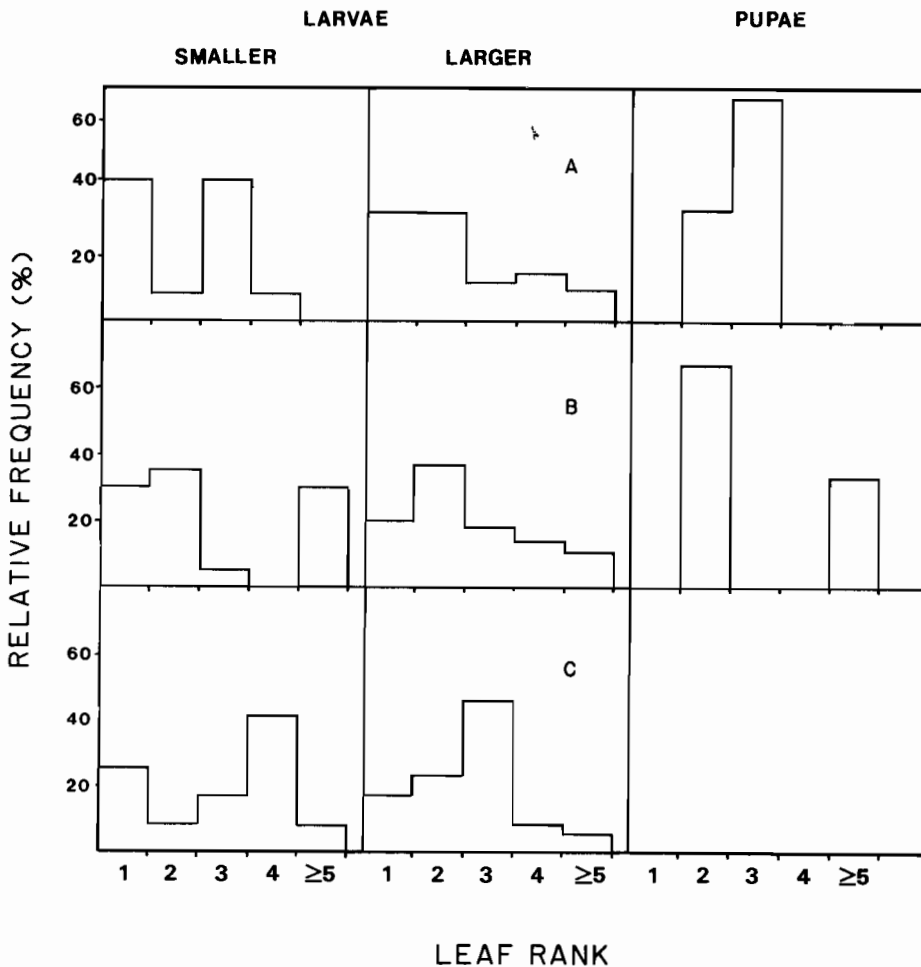


FIGURE 5. Relative frequency (%) of smaller and larger larvae, and pupae of midges in relation to host's leaf rank in: A) *H. nutans* (rainy season), B) *H. heterodoxa* (rainy season), and C) *H. heterodoxa* (dry season).

patterns of distribution among leaves in each pitcher plant. Midge pupae did not appear in the youngest leaves of the pitcher plants, and did not appear at all in the leaves of *H. heterodoxa* during the dry season (Fig. 5).

DISCUSSION

Ecological patterns of *Heliamphora* insects

Leaves of pitcher-plants are temporary aquatic habitats that originate when the leaves open, and eventually degenerate and disappear. Their associated aquatic insects must colonize, complete their preadult development, and emerge as adults before the aquatic environment becomes unsuitable. Using the first and second instar larvae of each species of mosquito as indicators of recent oviposition (Fig. 4), the results suggested that most mosquito colonization occurred in the youngest leaves of *Heliamphora*, or early in the life span of the leaf. The concentration of mosquito eggs observed in the youngest leaves of the plants coincided with the high frequency of early instars of mosquitoes in those leaves. On the other hand, the small larvae of midges did not show a clear pattern of distribution among leaves of different ages (Fig. 5) suggesting that there was no preference for ovipositing in leaves of a given age. Despite the lack of a clear pattern of midge oviposition, pupation occurred in leaves of rank-ages 2 and 3, similarly to mosquitoes that had colonized younger leaves (Figs. 4 and 5). The low abundance of both mosquito and midge pupae in older leaves may indicate deteriorating aquatic habitats.

The importance of leaf age was evidenced by the negative correlations between this variable and mosquito abundance for both mosquito and plant species in the dry and wet seasons. A concentrated oviposition in the youngest leaf of a plant necessarily facilitates the occurrence of a negative correlation between number of preadults and time, because the individuals eventually complete their development and emerge as adults, or die. Colonizing the habitat very early should be advantageous in temporary habitats where the probability of persistence decreases with time. Figure 1 showed that the frequency of leaves decreased with their age, probably as a result of leaf senescence. Symptoms of senescence were observed in leaves of rank-ages 4 and older whose upper parts had dried up. As in *Sarracenia purpurea* (Bradshaw 1983), older *Heliamphora* leaves may have lower capacities to attract and capture prey arthropods than younger leaves with intact tissues. The exploitation of food resources by the preadults in young leaves of *Heliamphora* where most captures may occur, and the possible decrease in prey acquisition should result in an impoverished habitat. Both factors, increased risks of habitat disappearance and decreased habitat quality with leaf age should be acting as selective agents against late insect colonizers in *Heliamphora* pitchers.

The patterns of mosquito and midge distribution and abundance among leaves of different ages of *Heliamphora* are comparable with those observed in the mosquito and midge species of *S. purpurea* from Massachusetts (Fish and

Hall 1978). In this community, mosquito females (*W. smithii*) discriminate among leaves of different ages and choose the youngest leaf to oviposit based on chemical cues present in the leaves of *S. purpurea* (Istock et al. 1983). Bradshaw (1983) explained this behavior as an adaptation to anticipate the appearance of prey captures because most oviposition occurred in the youngest leaves of a plant before any prey has been captured, and because late colonizers suffered increased mortality in older leaves due to food limitation. The similarity between ecological patterns of the aquatic insects of *Heliamphora* and *S. purpurea* may result from the existence of equivalent aquatic habitats and local selective forces acting on analogous insect species bearing similar preadaptations or adaptive responses.

Two pieces of evidence make us believe that the common preferences of pitcher-plant mosquitoes to oviposit in the youngest leaves of a plant have evolved independently in *W. smithii* on one hand, and in *W. zinzala* and *W. fishi* on the other hand. First, Istock et al. (1983) studied the genetic basis for this behavior in *W. smithii* concluding that it seems to be of recent origin, and proposed that this mosquito descended from a bromeliad inhabiting mosquito at a time when bromeliads and pitcher-plants overlapped in distribution. Secondly, Zavortink (1985) in his description of the new mosquito species of *Heliamphora*, placed these two species alone in a new subgenus (*Zinzala*), and concluded that *W. smithii* does not belong to the same lineage as *Heliamphora* mosquitoes. Hence, the

similarity in oviposition patterns between *W. zinzala* (*H. nutans*) and *W. fishi* (*H. heterodoxa*) may have resulted from common and recent ancestry, whereas the presence of a similar pattern in *W. smithii* may have resulted from convergent evolution.

The evolution of habitat selection where mosquitoes colonize the aquatic habitats before food resources become apparent is not unique to pitcher-plant mosquitoes, and is also present in the mosquito *W. ulocoma* that exploits the aquatic floral bracts of *Heliconia caribaea* (Zingiberales: Heliconiaceae) in northern Venezuela (Machado-Allison et al. 1983). *Wyeomyia ulocoma* oviposits inside unopened (youngest) bracts, already containing water, where food resources are apparent. Bracts of this plant share several habitat features in common with the pitchers of insectivorous pitcher-plants, such as their temporary nature, the secretion of water by the plant inside the bracts, and the supply of food resources that eventually decrease in time.

Although insect phenology in *H. nutans* and *H. heterodoxa* was similar, insect abundance differed between plants species in the wet season, and between the wet and dry seasons for *H. heterodoxa* (Fig. 2). The higher abundance of mosquitoes and midges of *H. heterodoxa* is related to the larger leaves of this plant which may contain more resources per pitcher than *H. nutans*. An interesting result was that despite the numeric differences in aquatic insects between *Heliamphora* species, the medians of the ratios mosquitoes:midges per leaf did not

significantly differ in the same rainy season. In other words, each community had the same proportional abundance of insect species or community structure. Quantitative differences in insect abundance is likely related to resource abundance (leaf size), whereas qualitative similarity in relative abundances may be related to comparable modes of insect resource exploitation and resource types (prey insects and water dynamics).

The results of the description of the insect community of *H. heterodoxa* during the dry season revealed important changes in insect abundance and phenology. Only mosquitoes suffered reductions in abundance, and although midge abundance was essentially the same, no pupae were present at this time (Figs. 2 and 5). Also, midges appeared segregated from mosquitoes toward older leaves in comparison with their distribution in the rainy season. This change in joint distribution was exemplified by the shift from a positive correlation between mosquitoes and midges in the wet season, to a negative correlation in the dry season. These results suggest that the dry season was a suboptimal period for the pitcher-plant inhabitants. The plant phenology also changed in the dry season (Fig. 1) with most leaves in old age classes completely dry and senescent.

The negative correlation between mosquitoes and midges in the dry season, when habitat conditions should have been worse than in the wet season, brings up the question of coexistence, and also whether such changes occurred because of inter-specific competition.

Our observations on *Heliamphora* insects and the information available from the studies on mosquitoes and midges of *S. purpurea* suggest that these insects partition the habitat in space rather than in time. Mosquito larvae occupy the volume of free water of the pitchers where they filter-feed and browse on submerged surfaces. Midges live burrowed into the sediment of accumulated prey corpses at the bottom of the pitchers and feed directly on them. Despite spatial partitioning, both species depend on the prey arthropods captured by the plant, and possibly on micro-organisms growing in that medium. Both, Buffington (1970) and Fish and Hall (1978) suggested that spatial segregation between mosquitoes and midges of *S. purpurea* must facilitate coexistence in these limited habitats. Bradshaw (1983) and Bradshaw and Creelman (1984) showed that intra-specific competition in these two insect species exceeds inter-specific competition, thus promoting coexistence. Notwithstanding, the extent at which ecological niche segregation can be sustained between coexisting species when the common resources become scarce is a subject that merits further investigation. In Bradshaw's results, *W. smithii* inhibited pupation of midges at high densities of the mosquito or when resources were likely scant. But, midges facilitated development of mosquitoes at high densities (Bradshaw and Creelman 1984). The segregation between mosquitoes and midges among leaves of *Heliamphora*, and the lack of midge pupae in the dry season, offers the basis to postulate an explanatory hypothesis based on inter-specific competition.

Insect richness and diversity in pitcher-plants

So far, most ecological patterns observed in the insect communities of *Heliamphora* have been contrasted only with those studied in *S. purpurea*. The reason is that *S. purpurea* is the only pitcher-plant species among the nine species of pitcher-plants of the nearctic to host an aquatic community containing mosquitoes and midges. The rest of *Sarracenia* species (McDaniel 1971) contain only semi-aquatic Diptera, mostly Sarcophagidae (*Blaesoxipha celarata*, *B. fletcheri*, *B. jonesi*, *B. rileyi*, and *Sarcophaga sarraceniae*; Riley 1874, Aldrich 1916, Stone et al. 1965), but also Phoridae (*Dohrniphora venusta*; Jones 1918), and Sciaridae (*Neosciara macfarlanei*; Jones 1920). The western pitcher-plant, *Darlingtonia californica*, contains only a species of Chironomidae (*Metriocnemus edwardsi*), and Chloropidae (*Botanobia darlingtoniae*; Jones 1916).

In addition to the mosquitoes (Culicidae) and midges of *S. purpurea*, this plant also hosts the sarcophagids *B. fletcheri* and *Sarcophaga sarraceniae*. On the other hand, the two neotropical *Heliamphora* species investigated here lacked sarcophagids or other semi-aquatic insects.

This faunistic comparison leads us to conclude that *Heliamphora* insect communities are richer in species than *D. californica*, but poorer in species than the insect community of *S. purpurea*. In the other *Sarracenia* species that only contain semi-aquatic insect species, insect richness varies, with *S. flava* and

S. minor being the richest with up to five insect species each, although probably not all these species occur simultaneously in either plant species, and most of these insect species are common to both pitcher-plants (Riley 1874; Hubbard 1896; Jones 1904, 1918, 1920; Aldrich 1916; Stone et al. 1965; Fish 1976).

Another aspect of this comparison is that the lack of sarcophagids in *Heliamphora* makes these communities not only less rich in insect species, but also less diverse in the type of insect species associated with the plants, as compared with *S. purpurea* which harbors mosquitoes, midges, and sarcophagids. The lack of sarcophagids from *Heliamphora* is intriguing, in particular because these insects are also found living in some tropical insectivorous pitcher-plants of the Old World, the Nepenthaceae, which host similar types of aquatic insects to those of the New World pitcher-plants (Beaver 1983). Neotropical aquatic insect communities living in *Heliamphora* are also poorer in species and less diverse than the species of *Nepentes* studied by Beaver (1983) in Malaysia. Since *Heliamphora* insect communities are less diverse than that of *S. purpurea* but richer than that of *D. californica*, we conclude that these aquatic communities do not follow the general tendency observed for most biotic communities of increased biotic diversity with decreasing latitude (Pianka 1966). Factors other than latitude that should eventually be investigated are plant phenology, leaf morphology, and altitude.

The lack of a direct taxonomic relationship between the nearctic

pitcher-plant mosquito, *W. smithii*, and the neotropical *W. zinzala* and *W. fishi* (Zavortink 1985), does not help on determining if the dispersion of the host plants from the neotropics into the nearctic was accompanied by their associated mosquitoes. Only if the nearctic mosquitoes had been closely related to *Heliophora* mosquitoes it would have indicated an original continuous distribution of the host-plants and inquiline insects.

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