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THE MAN-BITING ACTIVITY OF PHLEBOTOMINE SAND FLIES (DIPTERA: PSYCHODIDAE) IN A TROPICAL WET FOREST ENVIRONMENT IN COLOMBIA

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ABSTRACT

The purpose of this study was to investigate the temporal and spatial attributes of the man-biting activity of phlebotomine sand flies in a Tropical Wet Forest environment. The study was undertaken in a sparsely populated region of the east central portion of the Department of Antioquia, Colombia. With three two-man teams as bait, catches of approximately 10 hours duration during the day and approximately 13 hours for the night and twilight period were made at three separate forest locations and six diverse clearing sites. In the forest series of catches, the predominant man-biting species and their percentage of the catch were Lutzomyia hartmanni *(56%),* L. trapidoi *(22%), and* L. yuilli *(13%). In the clearing series of catches the predominant species were* L. hartmanni *(56%),* L. gomezi *(16%),* L. yuilli *(9%), and* Warileya rotundipennis *(9%).*

For most species, both the magnitude and vertical stratification of their man-biting activity tended to be quite variable between the three forest sites. These differences were thought to be related to local variations in forest structure. Between-site differences in the magnitudes of biting activity were least pronounced in the understory. L. trapidoi, *and to a lesser extent* L. yuilli, *were reluctant to bite at ground level in either the forest or clearing habitats. Their diminished biting activity at ground level appeared to primarily account for the greater similarity of the clearing catches to the forest floor catches than to those in the understory and canopy. In the clearing series of catches, the biting activity of* L. hartmanni, L. trapidoi, *and* L. yuilli *was detected to be significantly greater at the two forest edge sites than at those sites within the clearing. Diversity of man-biting activity in the clearing habitat was determined to be greatest at a site situated at the edge of pioneer vegetation and pasture. The pioneer vegetation extended to this location from the forest about 130 m away.*

The man-biting activity of phlebotomine sand flies in the Providencia study area was primarily nocturnal although crepuscular patterns were exhibited by L. bifoliata *within the forest and by* L. gomezi *at the clearing sites. The temporal pattern of biting activity of each of the predominant forest species, i.e.,* L. hartmanni, L. trapidoi, *and* L. yuilli, *was quite variable from one night to another and there was often a sharp peak in the biting activity. When such variations were averaged, the summarizing pattern tended to distort the true nature of the biting activity and only defined a rather broad interval of time in which biting activity was likely to be concentrated. There was no indication of a nightly pattern of vertical movement by any of these three species. The biting activity of most species appeared to be concentrated at a somewhat earlier time in the clearing habitat than in the forest.*

The magnitude of man-biting activity for all species combined was relatively uniform throghout the year; however, the dry season was unusually wet. Most of the individual species also did not appear to have pronounced seasonal fluctuations in biting acitivity although L. panamensis *was a notable exception.*

The patterns of man-biting activity exhibited by L. gomezi *suggest that it is the species most likely to transmit dermal leishmaniasis to man in the region where our study was conducted. The phlebotomine sand fly assemblage of the Providencia study area is compared with that described from other locations in Colombia and Panamá. For each of the common man-biting species in the study area, a review of the literature pertaining to their biology is included.*

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DISCUSSION

INTRODUCTION

In many parts of tropical America, a rapidly expanding human population has accelerated man's encroachment upon the lowland rain forest. Man's perturbation of the rain forest ecosystem may begin with selective tree cutting. This may soon be followed by the establishment of small clearings for crops and pasture. If these clearings are abandoned within a few years, pioneer vegetation quickly takes over and the lengthy (more than 100 years) process of secondary succession begins, eventually leading to another climax forest (Budowski 1963, 1965). More often, these small clearings are expanded, e. g., large areas have been and are continuing to be cleared and converted to pasture for cattle production in the Department of Antioquia, Colombia.

Such abrupt changes in the environment have enormous influence upon the local flora and fauna. To determine and describe the extent to which the mammalian, avian, and haematophagous dipteran assemblages and associated vertebrate viruses are altered by such severe ecological perturbations, an intensive study of these groups was made within a limited geographic area (the Providencia study area) located in the foothills of the Andes in the Department of Antioquia, Colombia. This study was conducted as part of an interdisciplinary research and training program established between the University of Wisconsin-Madison and the Veterinary Faculty of the Universidad de Antioquia in Medellín, Colombia. In the entomological portion of the investigation, an attempt was made to obtain an inclusive view of man-biting activity by all of the haematophagous Diptera within a Tropical Wet Forest environment; i. e., within both forest and clearing habitats. The present report is limited to the phlebotomine sand flies. Other families of haematophagous Diptera will be treated in forthcoming papers.

Phlebotomine sand flies are known to be vectors of cutaneous (including mucocutaneous) and visceral leishmaniasis in both the Old and New Worlds (Lewis, 1974). The epidemiologies, including incidence and distribution of human infections, of the eight *Leshmania* that infect man in the Western Hemisphere are reviewed by Ward (1976). Lainson and Shaw (1973) have revised the classification of the major species and subspecies of *Leishmania* occurring in the Americas and have enumerated the proven and suspected vectors of each form of cutaneous leishmaniasis. In the Neotropics cutaneous leishmaniasis appears to be endemic in many of the humid lowland forests (including the one in which the present study was made) occurring primarily as a zoonosis. In 1968, *World Health Statistics Report* indicated that from 1951 to 1965 there were 3,534 recorded cases of unspecified leishmaniasis in Colombia. Also, a number of arboviruses have been isolated from phlebotomine sand flies in Panamá (Test et al. 1974) and Colombia (Barreto 1969). Despite their importance in disease transmission, little information exists concerning the man-biting activity of Phlebotominae in Colombia. The most extensive observations appear to be those included in the primarily taxonomic work of Young (1971).

Our objective in this study was to determine the temporal and spatial attributes of the man-biting activity of phlebotomine sand flies in a Tropical Wet Forest environment. The daily periodicity (temporal pattern) of the man-biting activity of each of the common anthropophilic species was investigated. Comparisons were also made between three forest sites of the magnitudes of biting activity and patterns of vertical stratification of the predominant man-biting species. In addition, the forest series of catches provided some information about seasonal fluctuations in biting activity. Comparisons of man-biting activity were made between six clearing sites. The forest and clearing catches were differentiated as were the catches for the diverse microenvironments sampled within each of these habitats.

For several groups of haematophagous Diptera including the phlebotomine sand flies, attempts have been made to divide the Neotropical biogeographical region into areas of endemism or dispersion (Lane 1953, Forattini 1957, Bram 1967, and Martins and Morales-Farias 1972). These authors indicate that the region in which our study was located lies in an area of faunal transition. We have thus included a brief comparison of the sand fly fauna of the Providencia study area with those reported in the literature from neighboring regions. An excellent account of the speciation of forest birds in the tropical lowlands of northwestern South America is given by Haffer (1967). The area in which our study was conducted lies within the region described by Haffer as the "Nechí Refuge."

PREVIOUS STUDIES OF THE PHLEBOTOMINE SAND FLIES OF COLOMBIA

Previous studies of the phlebotomine sand flies of Colombia have been primarily descriptive and have been comprehensively reviewed by Osorno-Mesa et al. (1967) and Barreto (1969). In 1972 Osorno-Mesa et al. summarized and updated the literature on the Colombian Phlebotominae. Osorno-Mesa et al. (1967) provided a list of the 23 species identified from Colombia to that date, indicated their geographic distribution, and described a new species. Barreto (1969) reported the presence of 14 additional species which were collected from the Pacific lowlands near Buenaventura. Young (1971) listed 69 species from Colombia and provided a key to their identification along with detailed illustrations of most species. Seventy-six species were enumerated from Colombia by Osorno-Mesa et al. (1972a), who also recorded their geographic distributions. Recently, additional new species from Colombia have been described by Young (1973), Young and Porter (1974), and Morales-Alarcón et al. (1974).

There was little information prior to the late 1960's concerning the specific identity of the man-biting phlebotomine sand flies of Colombia. Osorno-Mesa et al. (1967) observed what they considered at the time to be *Lutzomyia verrucarum* (Townsend) biting man during both the dav and night in the Departament of Cundinamarca near the Río Bogotá at an altitude of 2,550m. Osorno et al. (1972b) showed that this was actually a new species which they named *L. andina*. From a series of collections made in the Pacific lowlands near Buenaventura in which humans were used as bait, Barreto (1969) observed the following species biting man: *L. olmeca bicolor* Fairchild and Theodor (reported as *L. flaviscutellata* [Mangabeira]), *L. hartmanni* (Fairchild and Hertig), *L. panamensis* (Shannon), *L. pessoana* (Barretto) (reported as *L. paraensis* [Costa Lima]), *L. trapidoi* (Fairchild and Hertig), and *L. ylephiletor* (Fairchild and Hertig). Man-biting catches were made at four locations in the Department of Chocó by Young (1971) as part of a general survey of the phlebotomine sand fly fauna of the region. These catches were made between March and December 1967 and apparently provide the only quantitative information about the man-biting activity of Phlebotominae in Colombia. Young's results are summarized in the discussion. Other anthropophilic species reported from Colombia include *L. yuilli* Young and Porter by Young and Porter (1972); *L. lichyi* (Floch and Abonnenc), *L. longipalpis* (Lutz and Neiva), *L. gomezi* (Nitzulescu), *L. columbiana* (Ristorcelli and Van Ty); *L. evansi* (Nuñez Tovar), *L. ovallesi* (Ortiz), and *L. shannoni* (Dyar) by Osorno-Mesa et al. (1972a): *L. cirrita* Young and Porter by Young and Porter(1974); and *L. disiuncta* Morales-Alarcón, Osorno, and Osorno-Mesa by Morales-Alarcón et al. (1974).

THE STUDY AREA AND ITS CLIMATE

The Providencia study area (Fig. 1) is situated in a hilly and sparsely populated region of the east central portion of the Department of Antioquia, Colombia. Our studies were made in the area surrounding the Providencia hydroelectric plant (lat. 7°19'N, long. 75°04'W) which was approximately 25 km south and 22 km west of Zaragoza, an important early center of Spanish gold mining activity. The study area lies within the foothills of the northern slopes of the central cordillera of the Andes, is drained by the Río Anorí, and varies in elevation from approximately 400 to 800 m.

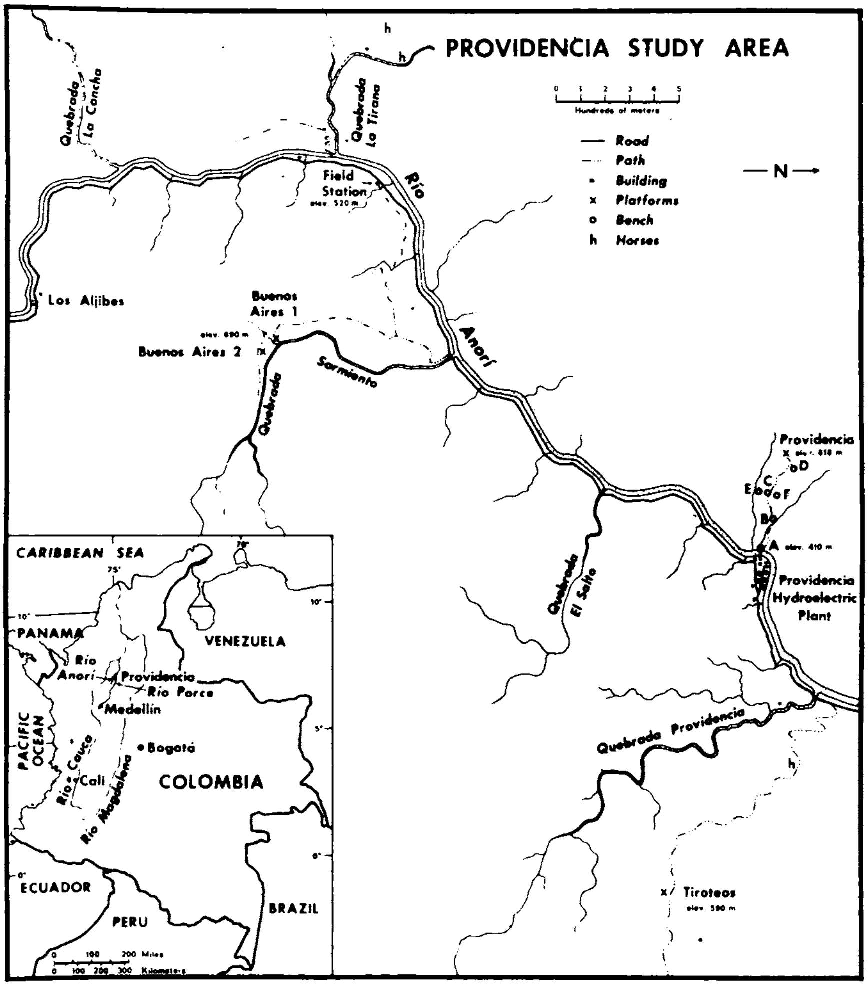

Fig. 1. The Providencia study area and its location in Colombia.

The steep slopes characteristic of large portions of the Río Anorí watershed have prevented large scale colonization of much of this region including the Providencia area. The hillsides facing the Río Anorí in the Providencia region are known to have been subjected to intermittent clearing since the 1930's and selective cutting since the 1900's. Large tracts of relatively undisturbed forest still exist and in general tend to become less disturbed as one moves away from the river. Relative inaccessibility and a very hilly topography have tended to discourage the use of the area for livestock production, although such an endeavor was being undertaken in 1971 near La Tirana. In addition to the 11 to 12 families associated with the Providencia hydroelectric plant, only a few subsistence *colonos* live in the Providencia region, and they reside primarily on the slopes facing the Río Anorí.

The Providencia region has a mean annual rainfall of 462 cm (Table 1), and there is a distinct tendency for this rain to occur at night. A dry season, characterized more by a reduction than absence of rain, usually occurs from December through March. No month has a mean rainfall of less than 9 cm. Daily rainfall exceeded 10 cm on three occasions in 1970 and seven in 1971. The unusually large amount of rain recorded during the 1970-71 dry season occurred while our

Table 1. Monthly and annual rainfall (in cm) recorded at the Providencia hydroelectric plant.

Year	Month												Annual
	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
Mean[a]	13.5	9.4	19.8	35.3	59.9	54.6	46.2	61.7	46.2	51.0	47.2	17.5	462.3
1970	16.3	11.2	21.1	48.3	45.2	70.1	48.3	82.6	57.9	37.3	38.4	36.8	513.5
1971	36.3	27.2	50.5	24.6	53.3	43.2	53.8	57.4	69.6	60.4	54.6	11.2	542.1

[a] Twenty-one year mean compiled from climatic records maintained at the Providencia hydroelectric plant by Pato Consolidated Gold Dredging, Ltd., for the years 1944-49 and 1957-71.

field studies were in progress and perhaps minimized the influence this period may have on the population levels of the haematophagous Diptera. The nocturnal pattern of rainfall is thought to be related to the geographic location of the Providencia region in the foothills of the central cordillera. A high annual rainfall which occurs primarily at night, an absence of a severe dry season, and a moderate elevation (400-800 m) all tend to promote a continuously high relative humidity in the Providencia region.

Hourly forest temperature means were compiled from readings obtained during the platform studies. The temperature measurements were made from a thermometer placed at a height of 0.7 m above the forest floor. The sharpest temperature changes within the forest occurred between 0800 and 1100 hours at which time the temperature increased about 2°C. A somewhat less pronounced corresponding decrease in temperature occurred between 1800 and 2000 hours. The temperature continued to fall slowly throughout the night, reaching a low at 0600 hours. The mean maximum temperature within the forest, based on 52 sets of observations taken over one year, was 25.2°C. A mean minimum forest temperature based on only half as many observations was 21.5°C. Temperatures at the Tiroteos site appeared to be about 0.5-1.0°C higher than at the Buenos Aires sites. The latter site was 100 m higher in elevation. Temperatures at the Providencia forest site tended to be somewhat intermediate, more closely resembling the Tiroteos site.

CLASSIFICATION AND GENERAL DESCRIPTION OF THE FORESTS IN THE PROVIDENCIA REGION.

Since the Providencia region has an estimated mean temperature of 23.1°C, an annual mean rainfall of 462 cm, and an elevation varying from 400 to 800 m, the forest would be classified according to the Holdridge Life Zone Chart (Holdrige 1947) as Tropical Wet Forest, cool transition (Holdridge et al. 1971). Most of the forested areas occurred on steep, well drained slopes. For example, the terrain of the Buenos Aires forest in the vicinity of the first platform site was quite variable with the direction of slope fluctuating from 60° east of north to 25° east of south and the angle of slope ranging from 19 to 70%. The soil of the Providencia region was derived from metamorphic parent material (Anon. 1969), and in the forests it tended to be acidic with low natural fertility.

On the basis of physiognomic characters, the forests of the Providencia study area tend to be rather intermediate between the Tropical Wet Forest and Tropical Premontane Wet Forest Life Zones (Holdridge et al. 1971). The Buenos Aires and Tiroteos forest sites had an upper closed canopy comprised of trees 22-30 m tall with occasional emergents to 35 m. The forest at the Providencia site appeared to be about 5-10 m taller. These heights are less than the 45-55 m tall upper canopy observed for the Tropical Wet Forests of Costa Rica by Holdridge et al. (1971) and are somewhat lower than that recorded for the Premontane Wet Forests. The difference in height may be attributable to the general steepness of the slopes upon which the forests of the Providencia area occur. However, the thicker trunks of large trees, large number of tree species, usually large number of palms, and limited distribution of tree ferns more closely align the forests of the Providencia region with the Tropical Wet Forest Life Zone. In addition to these characters, a generally sparse ground cover and relatively low density of epiphytic moss on trunks further distinguish the Providencia forests from the Tropical Premontane Rain Forest Life Zone.

The estimated density of trees (10 cm dbh [diameter at breast height] or more), 78.5/0.1 ha (73.1/10,000 sq ft) at the Tiroteos site and 81.6/0.1 ha (75.9/10,000 sq ft) at the Buenos Aires site, was somewhat greater than that recorded for the Tropical Wet Forests of Costa Rica by Holdridge et al. (1971) but less than that observed by Grubb et al. (1963) for lowland rain forest in Ecuador. Species diversity was great at all sites, e.g., within a 242 m^2 sample area at the Tiroteos site there were 35 species, 14 of which had a dbh exceeding 10 cm. The upper canopy of these forests was composed of many species including: *Anacardium excelsum* Skeels, *Caryocar costaricense* Donn. Sm., *Carapa guianensis* Aubl., *Dimorphandra pemigera* Tul., *Brosimum* sp., *Andira* sp., and *Ocotea* sp. The understory of all three forests included representatives of such genera as *Inga, Luehea, Miconia, Pouteria, Turpinia,* and *Xylopia*. Leaf fall during the dry season was not readily apparent although one of the *Caryocar costaricense* at the Bueno Aires site became partially deciduous.

The composition of tree species forming the upper canopy varied with each forest and these floristic differences seemed to partially account for certain physiognomic variations between the forests. The frequent occurrence of *Carapa guianensis* in the Providencia forest resulted in buttresses being a prominent feature of that forest. Buttresses were least noticeable in the Tiroteos forest where they were considerably reduced both in number and size. Herbaceous epiphytes and lianas were abundant on the upper and middle strata trees at the Buenos Aires study site. Bromeliads and Araceae were the predominant herbaceous epiphytic forms but ferns, orchids, and cyclanths were also common. Tank epiphytes were estimated to be about five times as numerous at the Buenos Aires site as at the south facing Tiroteos location. However, bromeliads were more conspicuous in the Tiroteos forest since many tended to occur at quite low levels on trunks, a phenomenon which may be attributed to the frequently more open canopy. Palms were most abundant in the Tiroteos forest where, with an estimated density of 1,529/ha, they were a conspicuous component of the understory. Some selective cutting for bridge ties is known to have occurred in the Tiroteos forest.

FOREST PLATFORM SITES

The platform collections were made at three different forest locations locally known as Buenos Aires, Providencia, and Tiroteos (Fig. 1). The distance between the Providencia and Tiroteos sites was approximately 1.8 km while that between the Buenos Aires and Tiroteos sites was about 2.7 km. The latter two locations were united by a vast expanse of forest extending unbroken for many kilometers to the east.

Two platform sites were constructed in the Buenos Aires region, but only one, Buenos Aires 1, was used for the night studies. Both of these sites were located in a small extension of undisturbed forest that merged to the south and west with secondary forest on the steep slopes facing the Río Anori. To the east undisturbed primary forest extended continuously for many kilometers. Approximately 200 m to the north of the Buenos Aires 1 site, there was a 3.5 hectare fern-shrub thicket.

The Buenos Aires 1 platform site (Fig. 2) occurred on a narrow ridge near the top of a steep southeast facing slope at an elevation of 690 m. A small creek passed within 20 m of the site and joined a rapid stream about 50 m away. The understory and canopy platforms were constructed in separate trees of *Caryocar costaricense* Donn. Sm. which were 9 m apart. These platforms were at heights of 6.4 m (21 ft) and 16.2m (53 ft). The tree containing the upper platform was 27 m tall,

Fig. 2. The understory platform at the Buenos Aires 1 forest site.

and the crown of both trees supported a heavy load of herbaceous epiphytes including many large bromeliads.

About 90 m to the southeast and at the same altitude a second platform site, Buenos Aires 2, was constructed on a steep, approximately 50° , north facing slope. A 15 m wide clearing for power lines passed through the forest within 30 m of this location. The platforms were built in a tree known locally as "granadejo" and were at heights of 4.3 m (14 ft) and 13.4 m (44 ft). Unlike the platform trees at the Buenos Aires 1 site, the crown of this tree did not have a profuse growth of herbaceous epiphytes.

The Providencia platform site (Figs. 3 and 4) was located on a steep east facing hillside overlooking the hydroelectric plant at Providencia (Fig. 5). The lower two-thirds of this hillside was first cleared between 1941 and 1943 and now contains several vegetative formations including pasture, mixed pineapple-plantain cultivation, and secondary forest. This area will be described in more detail later in relation to the clearing sites. A slightly disturbed primary forest extended along the upper one-third of this hillside, but the west facing slope had recently been cleared for pasture. The forest was only about 200 m wide above Providencia but became more extensive to the southwest, reaching the river in several locations.

A platform site was constructed within the Providencia forest about 50 m from its lower margin with the clearing. The elevation at this level was 618 m, and the slope was gentle, about 20°, although most portions of the hillside were steeper, varying from 45° to 70°. The platforms were built in a buttressed, 39 m tall *Carapa guianensis* Aubl. at heights of 6.6 m (21.5 ft) and 18.6 m (61 ft). Only a few herbaceous epiphytes occurred in the crown of this tree.

Early differences in the populations of haematophagous Diptera observed between the Buenos Aires and Providencia locations prompted the construction of a platform site in a third forested area known as Tiroteos. This platform site was situated about 1 km inside an extensive tract of forest which merged with the Buenos Aires forest and extended for many kilometers to the east. The platforms were built in a large *Dimorphandra pemigera* Tul. (J.S. Denslow, personal

Fig. 3. The canopy platform at the Providencia forest site.

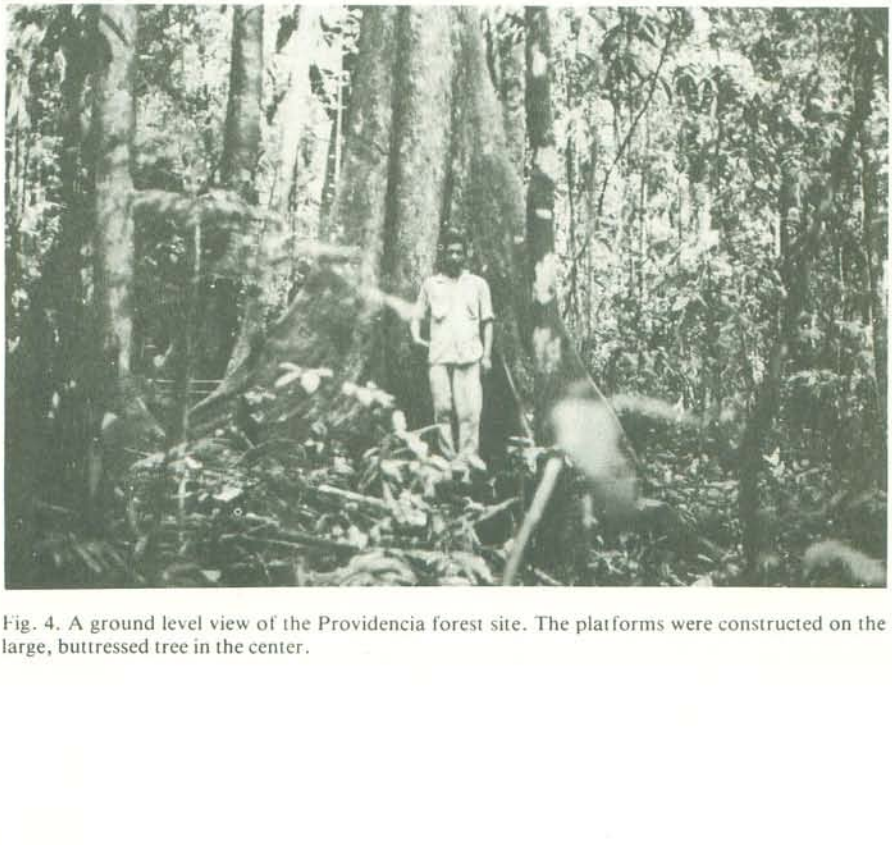

Fig. 4. A ground level view of the Providencia forest site. The platforms were constructed on the large, buttressed tree in the center.

Fig. 5. The Río Anorí valley at the Providencia hydroelectric plant. The clearing (bench) sites were located on the hillside in the background and the Providencia platform site was located in the forest above the clearing.

communication) which was located close to the top of a steep, approximately 45°, south facing slope at an elevation of 590 m. With an estimated height of 27.4 m this tree was a constituent of the upper canopy but had only a few herbaceous epiphytes and none of these were tank bromeliads. The platforms were placed at heights of 6.4 m (21 ft) and 18.0 m (59 ft).

CLEARING SITES

All six of the clearing sites were located in the extensive open area below the Providencia forest platform site (Fig. 5). This area, located on the eastern slope of the hill directly across the Río Anorí from the Providencia hydroelectric plant, was originally cleared between 1941 and 1943. Various portions of this hillside have been used in a variety of ways so that several kinds of vegetative formations were present at the time of our study. The collecting sites were so arranged as to occur in these major vegetative formations. Four of the six collecting sites, A through D (Fig. 1), were placed at approximately 60 m altitudinal intervals beginning with site A at the base of the hillside adjacent to the Río Anorí. Sites E and F were located at the same altitude as site C but were situated at the southern and northern edges of the clearing, respectively. Each of these collecting locations contained a bench shaded by a thatched roof; hence, they were referred to as bench sites.

Bench site A, elevation 420 m, was situated next to the Río Anorí across from the Providencia hydroelectric plant. This site was at the edge of a wooded area which extended uphill to the west. This woods was comprised of trees, including *Cecropia* spp., ranging in height to 12 m and had a thick undergrowth. The bench site was shaded after 1400 hours. The site was about 8 m above the river bed and faced 80° east of north toward several houses, the closest being less than 40 m away. A fast flowing creek emptied into the Río Anorí about 12 m upstream from site A.

Bench site B, elevation 470 m, occurred in an area of diverse cultivation (Fig. 6) approximately 120 m west-northwest of site A. To the north, a large cleared area planted with corn *(Zea mays* L.) extended to within

Fig. 6. An area of diverse cultivation in which clearing (bench) site B was located. Note the dense growth of pioneer vegetation among the plantains and fruit trees.

approximately 40 m of the site, and a small creek passed within 12 m to the northeast. In October 1970 a clearing, about 55x65 m, was made just to the south of the bench site and was planted with corn and pineapple *(Ananas comosus* Merr.), but by August 1971 many herbaceous pioneer species had become established, producing a very thick growth to a height of 2 m. The bench site itself was located within a small grove of diverse fruit trees but some plantains *(Musa paradisiaca* L.), yucca *(Manihot esculenta* Crantz), and pineapples were also present. The bench was constructed beneath a zapote tree *(Matisia cordata* Humb. and Bonpl.) which shaded the site throughout the day. An extensive area of plantain cultivation extended for about 80 m to the west. Some plantain and pineapple cultivation occurred to the east but soon merged into a thick growth of pioneer and early secondary vegetation.

Bench site C, elevation 540 m, was situated centrally in the lower half of a pasture, approximately 110 m west-southwest of site B. This site was fully exposed although there was a small clump of trees about 35 m to the west near the center of the pasture. An area of plantain cultivation occurred approximately 30 m to the east of the bench site. About 40 m north of bench site C the pasture merged with an extensive area of pioneer vegetation, and a 10-15 m tall early secondary forest (Budowski 1965) was located 40 m south of the bench site. The vegetation of the pasture consisted primarily of grasses and some herbaceous dicots and frequently reached a height of 1 m.

Bench site E, elevation 540 m, was located to the south of bench site C. It was situated just within the pasture at its margin with the 10-15 m tall early secondary forest. In the late afternoon the bench site became shaded by the forest. About 15 m to the south of the bench a rapid creek passed through the secondary forest. This forest merged about 100 m to the west with the mature forest containing the Providencia platform site.

Bench site F, elevation 540 m, was situated about 40 m to the north of bench site C and was at the edge of the pasture and a strip of late pioneer vegetation ranging in height to 9 m. The rather narrow, sinuous band of pioneer vegetation extended upward to the forest margin about 130 m to the west. A small creek passed bench site F about 65 m to the northeast and pioneer vegetation grew on the steep slope between this bench site and the creek. Bench site F, like site C, was thus not shaded by trees.

Bench site D, elevation 600 m, was located at the extreme northwest edge of the pasture, adjacent to the tall, mature forest containing the Providencia platform site. The bench site was situated at the tip of a small protrusion of the pasture into the forest. It was thus surrounded on three sides by forest and consequently was shaded by early afternoon. One creek passed approximately 90 m to the southwest of this bench site and a second, about 110 m to the northeast. The forest platform site was about 40 m to the southwest of this bench site.

The location of the bench sites may be summarized as follows: site A, edge of river and early secondary woods; site B, area of extensive and diverse cultivation; site C, open pasture; site D, edge of pasture and mature forest; site E, edge of pasture and early secondary forest; site F, edge of pasture and pioneer vegetation extending from forest. Since all of the sites were situated on the eastern slope of the hillside, they became shaded in the late afternoon when the sun passed behind the top of the hill.

MATERIALS AND METHODS

COLLECTING METHODS AND NUMBER OF CATCHES

Collecting methods. At each of the three forest platform sites six men were employed. This permitted the simultaneous collection of biting Diptera by two men at each of the three levels. The two-man teams rotated between the canopy, understory, and ground level at 2-hour intervals in order to minimize the effects of difference among workers both in their attractiveness to the Diptera and in their collecting ability. Kettle and Linley (1967) and Kettle (1969) have shown that substantial differences may occur between workers in their attractiveness to Ceratopogonidae, and they have calculated correction factors for each worker. We did not attempt to determine such differences between workers since it was not possible to retain the same six collectors throughout the period of this study. While collecting, the workers wore short sleeve shirts, rolled their pants up above their knees and did not wear shoes. All specimens landing on the workers were collected individually in either 1-dram or 5-dram vials depending upon the size of the insect. In some of the later catches, aspirators were used. To relate the specimens to the capture site, level, and time of collection, at the end of each catch period at each level all of the vials containing specimens were placed in a plastic bag labelled with the date, catch period, and level. For the night catches each collector used a flashlight which had its front glass covered with red cellophane to minimize the attraction of insects to light.

Duration and number of catches. Numerous workers studying the periodicity of biting activity of haematophagous Diptera (Lumsden 1952, Kettle and Linley 1967, Chaniotis et al. 1971b) have related the time of their collection periods to sunrise and sunset. Haddow (1954) has shown the value of obtaining an activity profile corresponding to the 24 hours of the day while at the same time maintaining similar light intensity relations (see Williams 1939) for each of these periods throughout the year. Hence, at the latitude of Providencia, 7° 19'N, the time period between sunset and sunrise was divided into 12 periods of equal duration as was the period between sunrise and sunset. These periods usually differed in length from the normal 60-minute hour. Such a division insured that the times of sunrise and sunset and their accompanying rapid changes in light intensity did not fall into two different catch periods at different times of the year. The times of sunrise and sunset for the latitude and longitude of Providencia were obtained from a table prepared for us by the Nautical Almanac Office, U.S. Naval Observatory, Washington, D. C. The time of sunrise in the Providencia region varied from 0542 to 0619 hours, and the time of sunset varied from 1739 to 1821 hours. The maximum length of each daylight catch period was 63 minutes and the minimum was 58.5 minutes; conversely, the maximum length of each night catch period was 61.5 minutes and the minimum was 57 minutes.

The series of nocturnal catches considered in this study began with a collection in late July 1970 at the Buenos Aires 1 site. This was followed by two collections per month for the remainder of the year. One of these collections was made each month at the Buenos Aires 1 site while the other collection alternated between the other sites. In 1971 a collection was made at each of the three sites every month through August. In addition, 58 daytime forest catches were made between May 1970 and July 1971. A series of 12 night catches was made between March and August of 1971 in a clearing adjacent to the forest in which the Providencia platform site was located. An extensive series of 65 daytime catches was also made in this clearing from October 1970 to August 1971.

The diurnal platform collections were 10 catch periods in length, extending from approximately 0700 to 1700 hours. The nocturnal collections extended from 1700 to 0600 hours and thus included the last daylight period in addition to all 12 night periods. The first daylight period, approximately 0600 to 0700 hours, was not sampled since it would have been necessary either to extend the already excessively long night collections or have the workers reach the relatively remote platform sites in the dark over difficult uphill trails. Continuous collections for 24 or more hours similar to those of Haddow (1954) were economically unfeasible.

Although heavy rains were infrequent during the day, they were of common occurrence at night during the rainy season and often prevented collecting on the exposed platforms for portions of the night. The decision to stop collecting during periods of heavy rain rather than construct roofs over the platforms was made primarily on account of the severe lightning that frequently accompanied these rains. Catch periods in which heavy rains occurred have been excluded from the data used to calculate the means. Since the bench sites had roofs, rain did not interrupt any of the collections made in the clearing.

Clearing catches Although there were a few differences, the general procedure used for the clearing catches was similar to that for the forest studies. The catches in the clearing were all conducted at ground level and were made by the same six collectors who participated in the forest studies. To facilitate comparison with the forest series of catches, the collectors worked in pairs, and this resulted in the simultaneous sampling of three sites. Therefore, the clearing collections were made on two consecutive days with sites A, B, and D being sampled on the first day. Aspirators were used in making the night collections, and all specimens were chloroformed and preserved in 70% ethanol.

SPECIES IDENTIFICATION

The majority of the Phlebotominae obtained from the platform collections were separated into groups for attempted virus isolation based on their external appearance. Since these superficial groupings often contained more than one species, we also cut off the posterior abdominal metameres containing the spermathecae. These metameres were stored in appropriately labeled shell vials containing a mold inhibitor. After returning to Wisconsin, the pooled specimens were identified by clearing the metameres in 10% KOH and examining the spermathecae in a depression slide containing lactophenol tinted with iodine. In addition, representative specimens from each collection along with any unusual specimens were preserved by layering in pillboxes. All of the specimens taken from the clearing sites were preserved in alcohol. These specimens were more satisfactorily cleared by placing them in beechwood creosote for 2 days before they were cleared in 10% KOH.

External morphological characters and color patterns were used by us to group or distinguish the specimens in the biting catches, although the specific identification of each species was ultimately based on their spermathecae and other structures requiring high power magnification. Chaniotis (1974b) has recently outlined the problem of identifying phlebotomine sandflies on the basis of external characteristics and has provided a key to separate the anthropophilic species in Panamá.

Warileya rotundipennis Fairchild and Hertig was readily distinguished from the other man-biting species by its distinctive wing shape and uniformly tan appearance. *L. olmeca bicolor* Fairchild and Theodor was identified by its very distinctive color pattern (Chaniotis 1974b). The combination of pale wing scales and infuscated mesonotum distinguished *L. hartmanni* from the other common man-biting species. Although *L. cirrita* resembled *L. hartmanni* in external appearance, it was recognized by its large size and paler mesonotum. *L. sp.* near *osornoi* (Ristorcelli and Van Ty) was another *vexator* group species that was occasionally taken in the biting catches. Superficially, this species is very similar in appearance to *L. hartmanni* although the longer fifth palpal segment permits its separation under high power magnification. Careful examination of eight forest catches which had been preserved in their entirety and all of the clearing catches indicated that this species was rare, but undoubtedly a few have bee misidentified as *L. hartmanni*.

L. trapidoi and *L. yuilli* were readily distinguished from the other common species by their pale mesonotum, grey wing scales, and small size. However, we were unable to distinguish these two species by external appearance. Since *L. trapidoi* and *L. yuilli* were not distinguished in the first three night catches, these catches were not included in the tabulations of these two species. A total of 645 specimens of these two species, the majority of which were engorged, were not identified, and thus it was necessary to apportion these specimens to the period in which they were caught according to the ratio of known specimens in that catch period. A final group characterized by an infuscated mesonotum and dark wing scales was comprised of *L. panamensis*, *L. ayrozai* (Barreto and Coutinho), *L. gomezi*, and *L. bifoliata* Osorno-Mesa, Morales-Alarcón, de Osorno, and Muñoz de Hoyos. Subsequently we were able to separate these species according to the length of their fifth palpal segment and the color of the pronotal lobes. *L. gomezi* and *L. bifoliata* have long fifth palpal segments, whereas *L. panamensis* and *L. ayrozai* are members of the subgenus *Psychodopygus* and have very short fifth palpal segments. The pronotal lobes of *L. ayrozai* and *L. gomezi* were almost white while those of the other two species were infuscated and concolorous with the mesonotum.

DATA ANALYSIS

Logarithmic transformations. Logarithmic transformations (log$_e$) of actual catches were frequently used in the analyses presented in this paper. The antilogarithm of the arithmetic mean of logarithms of a set of numbers is the geometric mean of these numbers. Since the catch of a particular species sometimes was zero, log (x + K), where K equals some constant, was used instead of log (x) to avoid the problem $\log (0) = -\infty$. When there was a conversion to antilogarithms the constant (K) was subtracted from the antilogarithm. The result is close to the geometric mean provided that a relatively small constant is used. The use of logarithmic transformations for the analysis of biting cycles has been discussed by Haddow (1954). Insect catches tend to be quite variable in magnitude and between catch differences are often of a multiplicative (geometric) nature (Williams 1937, 1951). Through the use of the geometric mean, the influence of very large catches is reduced since the proportion $\frac{\log x}{x}$ decreases with increasing size of x, where x is any number greater than 3.

In many of the tables summarizing the catches, the results were presented both as absolute numbers and as modified geometric means. Individual catches were transformed to logarithmic values (Haddow 1954, 1960). The terminology of Haddow (1960) and Kettle and Linley (1967) has been adopted for those portions of the study where the additive constant was consistently 1.0. The symbol M_L represents the mean log catch:

$$M_L = \frac{\Sigma \log (x+1)}{n}$$

where n is the number of observations. M_W represents the modified geometric mean: M_W = (antilog M_L) -1. In this paper M_W is the modified geometric mean catch per period. Log (x + 1) has the desired effect or resembling a square root transformation for numbers up to 10 and being similar to log (x) for greater values (Steel and Torrie 1960). The modified geometric mean catch per night for a given site and level was used for the statistical analyses.

Temporal patterns. The graphs of the summary temporal patterns of biting activity were constructed from the modified geometric means of the catch periods (M_W). These means were reduced to percentages (Haddow 1960) to facilitate comparison of the temporal patterns between both species and habitats. When the summary temporal pattern of biting activity was partitioned by vertical level (Fig. 19), the modified geometric means were not reduced to percentages as we were interested in the magnitude of the differences between levels.

The graphs of the temporal patterns for individual nights were derived by converting the number taken during each catch period to a percentage of the entire night's catch. Averaging techniques such as running means or the modified geometric mean of the three vertical levels were not used as they frequently caused excessive distortion of these temporal patterns.

As mentioned earlier, the night catches consisted of 13 consecutive periods and included the last daylight period. Although phlebotomine sand flies were seldom encountered during the last daylight period, it is included in the tables and graphs of the temporal patterns of biting activity but is omitted from the other tables concerned with nocturnal biting activity and from the statistical analyses.

Between-site analyses of the clearing catches. A small series of night catches was made at the six clearing sites to provide an indication of Phlebotominae man-biting activity in a variety of vegetation formations located at varying distances from the forest. First, the null hypothesis of no difference in biting activity between the clearing sites was tested for each of the six most abundant species and for the entire population. A two-way analysis of variance with a randomized complete block design was computed for each of the species and for the entire population. Differences between catches may be of a geometric rather than additive nature (Williams 1951). Since the standard analysis of variance model assumes the components of the variance are additive, the precision of this analysis is likely to be reduced if they are multiplicative. Therefore, Tukey's test of non-additivity (Snedecor and Cochran 1967), in conjunction with some preliminary two-way analyses of variance, established the necessity of a logarithmic transformation to produce additivity. Along with additivity, the logarithmic transformation tended to bring about a closer approximation to normality and equality of variance. To avoid the problem of zero values, a constant of either 1.0 or 0.1 was added to each of the values used in the analyses before the transformations were made. The constant used for a given species was also determined by Tukey's test of non-additivity. The observations used in the analysis of variance for a given species were thus the transformed sums of the specimens taken on each of the nights at each of the sites.

For those species with statistically significant site F ratios, $P \leqslant 0.05$, all 15 simple differences between sites were tested for significance as was the contrast between the two forest margin sites, D and E, and the four sites within the clearing. The multiple comparison method of Scheffé was used as it allows one to make every contrast of interest without increasing the probability of declaring a contrast significant when it is not (Miller 1966, Nemenyi 1968). This test may be expressed as

$$\frac{\Sigma c_i \bar{x}_i}{\sqrt{\left(\Sigma \frac{c_i^2}{n_i}\right)\hat{\sigma}^2}}$$

where the c_i's are linear coefficients which add up to zero, $\Sigma c_i = 0$; the $\bar{x}_i$'s are the means to be tested; n_i denotes the number of catches in the category whose mean is $\bar{x}_i$ and $\hat{\sigma}^2$ is the estimated variance. In those instances in which the contrast between the two groups of means (i,e., D + E vs A,B,C, and F) was significant, confidence limits were constructed according to the method of Scheffé. The confidence intervals of all contrasts have half-lengths $SE\sqrt{(k-1)F_\alpha}$ where SE is the estimated standard error, K represents the number of means which can be compared, and F_α denotes the critical value of F for a desired probability with degrees of freedom from the analysis of variance for the means being tested and error (Nemenyi 1968).

For each species the pattern of its biting activity across the six clearing sites was compared with the pattern of each of the other five prevalent species. The abundance of each of these species in relation to each of the others was also determined. Again, two-way analyses of variance with randomized complete block designs were used, but the analyses were made on log ratios, i.e., the log transformed sum of specimens of one species taken from a given night and site minus the log transformed sum of another species for the same night and site. Thus, the analysis of variance F ratio for testing equality of site means becomes a test for interaction between species and sites and detects whether there is a significant difference between the patterns of biting activity of any two given species across the six sites. In other words, a significant F ratio indicates that the abundance ratio of the two species fluctuated significantly between sites. When the F ratio was significant, 95% confidence intervals based on the *t*-distribution were calculated for the abundance ratios of each site, providing an indication of the relative abundance of one species to another. Allowance could be made for the multiple comparisons, i.e., six comparisons for the above instance, that would widen the confidence intervals. However, these comparisons are between means of catches made in the field under the influence of a number of undefined environmental and physiological variables so that an allowance for multiple comparisons would be of doubtful value. A single confidence interval for all sites was calculated when the F ratio for interaction between sites and two species was not statistically significant. In computing this confidence interval, the total mean square was used as an estimate of variance. The main effect F ratio indicated whether there was a significant difference in the amount of biting activity between any two species. The 95% confidence interval for all sites included 1.0 (ratio 1:1) whenever the main effect F for difference in abundance was not statistically significant.

Estimates of the diversity and evenness of man-biting activity. The degree to which the various species of phlebotomine sand flies were attracted to a human host is not known. Thus estimates of sand fly diversity at the six clearing sites cannot be made from the catches. However, estimates of the diversity of the biting activity at the various sites can be made using

$$\hat{H}' = -\Sigma_i \frac{X_i}{X} \log_e \frac{X_i}{X}$$

where X_i is the total catch of species i over all the observations, and X is the total catch of all species over all the observations. This formula gives a biased (statistical sense) estimate of H', but is satisfactory for the purpose of comparing diversity of biting activity between the six clearing sites.

The evenness or equitability index J' (Pielou 1969) was used as it appears to be less dependent than other measures on the observed number of species when the number is small, especially when it is less than ten (Sheldon 1969). The number of species taken at the six sites varied from 6 at site A to 11 at site E.

Between-level and between-site analyses of the forest catches. Analysis of the night forest catches has been complicated by missing observations which were primarily caused by interruptions in collecting due to heavy rains. As a result, the 12 catch periods have unequal numbers of observations. Since catches in the forest were conducted simultaneously at three levels, they were all discontinued at the same time; thus an equal number of catch periods was maintained for each level. Catches were made at only two forest sites per month from September 1970 to December 1970 resulting in an unequal number of catches between the sites.

The null hypothesis of no difference in man-biting activity between the three forest levels was tested by means of a nonparametric rank test for comparing all possible pairs of treatments (Wilcoxon and Wilcox 1964). Briefly, for *p* treatments and *n* repetitions of the *p* treatments, rank numbers are assigned for each *p* of a given repetition. In our case, 0 was assigned to the smallest value and a rank of 2 was given to the largest. The assignment of ranks is repeated *n* times. The sum of the ranks for each treatment is obtained and all possible differences among these sums are computed. For *n*'s of 25 or less, these differences may be compared with critical differences associated with specific probabilities in a table (Wilcoxon and Wilcox 1964). Alternatively, these differences for any *n* may be divided by their standard deviation and compared with a table of critical values for rank sum tests adjusted for making any and all comparisons among several means (Nemenyi 1962). The degrees of freedom used are "very many" because of known variance. The standard deviation of a difference between three ranks may be expressed as $\sigma_d = \sqrt{2np(p+1)/12}$ which reduces to $\sqrt{2n}$. The occurrence of ties is not assumed with this standard error formula, although a good approximation is achieved when only a few are present. To minimize this problem, we omitted those instances in which all three levels of a given repetition were zero.

The null hypothesis of no difference in man-biting activity between the three forest sites was tested for all species combined and for *L. hartmanni, L. trapidoi,* and *L. yuilli.* An analysis of variance with a factorial design was computed for each of these three species and for the entire population. These analyses were complicated by an unequal number of observations both between catch periods and between sites. To reduce the amount of missing data, i.e., the number of catch periods with missing observations, only the first seven catch periods were used for the analyses. This diminished the percentage of catch periods with missing observations from 22% to 13%. Missing observations in the last five catch periods were especially numerous for the Buenos Aires 1 site where values were present for only half of the periods. When an observation was missing from one or more of the first seven catch periods the mean of the values present was computed. This mean was then substituted for those catch periods with missing observations. When observations were missing they varied from one to three, although there was an instance where four and another where five observations were absent. The creation of a mean from six values on some occasions and from five or four on others does introduce an additional source of error into the analyses.

A general analysis of variance program, NWAY1, from the STATJOB series available from the University of Wisconsin-Madison Academic Computing Center was used for the analyses. The number of catch nights for the forest studies varied by site so that there were 14 for Buenos Aires 1, 11 for Providencia, and 10 for Tiroteos. For instances like this where there are an unequal number of replicates between cells, NWAY1 does an approximate unequal cell analysis using Scheffé's approximation.[1] The number of catch nights used for the analyses of *L. trapidoi* and *L. yuilli* were reduced by two for the Buenos Aires 1 site and by one for the Providencia site. The transformation $\log_e (X + 1)$, where X is the sum of the seven catch periods, was applied to each replication before the analyses of variance were performed.

Comparisons between sites were made from the transformed site means for each level and for the there levels combined. The multiple comparison method of Scheffé was used for making the contrasts between pairs of means as it provides extra allowance for selection in multiple comparisons. This test has already been described in relation to the clearing data. The estimate of variance required for this method was the mean square variation within cells from the analysis of variance. The Scheffé critical values of t were derived from $\sqrt{(k-1)\,F_\alpha}$ where *k* is the number of means which can be compared and F_α denotes the critical value of F for a desired probability with degrees of freedom from the analysis of variance for site and variation within cells (Nemenyi 1968). Since the comparisons between sites were made for each of the three vertical levels, the critical values of F used in the above formula were $\alpha = .05/3$ and $\alpha = .01/3$. This allowance, derived from the Bonferroni inequality, was made to insure that the error probability per analysis did not become greater than .05

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[1] Henry Scheffé, *The Analysis of Variance* (New York: John Wiley and Sons, Inc., 1959), p. 362 - 63.

(Nemenyi 1968). This allowance was not used for calculating the Scheffé critical values for the comparisons for all levels combined. For these comparisons the critical values of F were $\alpha = .05$ and $\alpha = .01$.

The analyses of variance computed from NWAY1 (Table 9) also provide an F ratio for levels. However, multiple comparisons between levels were not made since such comparisons have already been tested by the nonparametric rank method described earlier.

Polar ordination analyses. In an attempt to better understand the distribution of the man-biting Phlebotominae species over the variable microenvironments sampled, a polar ordination analysis of the Bray and Curtis (1957) type was applied to the series of night catches made at the forest and clearing sites. Over the past 15 or so years, polar and principal component ordination techniques have become widely used in the analysis of plant communities (Beals 1973). Helpful introductions to these methods are presented by Allen and Skagen (1973), Orloci (1966), and Anderson (1971).

Ordination techniques position a series of points, which may represent species, samples, or environmetal factors, in an N-dimensional abstract space utilizing geometric principles. The dimensional framework may likewise be species, samples, or environmental factors so that a number of species may be placed as points in sample space or a series of samples may be place as points in species space. The distances between a series of points in an N-dimensional space are a measure of their difference. When the multidimensional space is reduced to one, two, or three dimensional space for the purposes of simplification, clarification, and graphing, a certain amount of variation i.e., information, is lost. However, the new axes are chosen to minimize loss of ecological information.

A total of 132 entities (catches) were considered. The series of 32 catches made in the forest over a year's time were separated by level, thus accounting for 96 of the entities. The remaining 36 represent the catches made in the clearing between March and August of 1971 as previously described. The eight most abundant species (attributes) were used to characterize the entities. A sum for each of these species was obtained for a night's catch at a given site. These sums were transformed to square root values in order to reduce the influence of *L. hartmanni* which accounted for over half of the specimens taken. Considerable ecological information about an entire system may be derived from certain indicator species (Allen and Skagen 1973) which may not be the most abundant. Since the catches were not all of equal duration, the eight square root values of each entity were relativized, giving the percent contribution of each species to the total catch which sums to 1.0.

Intercatch distances were calculated from the dissimilarity measure $1\text{-}2w/(a+b)$. This distance measure is based on the coefficient of similarity $2w/(a+b)$ used by Bray and Curtis (1957), where a is the sum of the quantitative scores of species in one entity, b is the sum of the quantitative scores of species in another entity, and w is the sum of lesser quantitative scores of species common to both entities. In this analysis the dissimilarity measure actually becomes $1\text{-}w$ since after relativization the total score of each entity was 1.0. Beals (1973) has reviewed the objections to the use of this distance measure and has concluded that the results obtained from a Bray and Curtis type of ordination using the above distance measure have been more ecologically informative than those obtained from more sophisticated methods such as principal components analysis.

Once the intercatch distances have been calculated an axis is constructed on which the entities are positioned. The entities chosen as endpoints for the first axis could be those with the greatest intercatch distance which is essentially the method used by Bray and Curtis (1957). Since ecological information may be obscured by the influence of unusual stands when this method of endpoint selection is used, Beals (1973) has suggested that different criteria for endpoint selection, such as using two dissimilar entities with large variance in their distances with other entities, may be more appropriate. Thus in the method used by us, the entity chosen as the first endpoint was the one whose matrix of distances from the other entities had the greatest variance. Before the variance of each entity's distance matrix was computed, zero values were removed from the matrix. In determining the second endpoint, a regression of the distances of a given entity to all other entities was made against the corresponding distances from the first endpoint. This was repeated for each of the other entities and the entity with the lowest regression coefficient was selected as the second endpoint. The method of Bray and Curtis (1957) and Beals (1960) was used for the orthogonal projection of the entities onto the first axis.

The construction of the second and third axes was accomplished by using residual distance matrices as suggested by Beals (1973). The distance between two entities on the first axis represents an orthogonal component of the entire intercatch distance between these two entities. The remaining orthogonal component, i.e., the residual distance, can be determined from the Pythagorean theorem as follows:

$$h_j = [d^2_{1j} - (x_{1j} - x_{2j})^2]^{1/2}$$

where d_{1j} is the distance between the two entities (for computing residual distances from the first axis, this is the intercatch distance derived from the dissimilarity measure) and the hypotenuse of a triangle with $x_{1j} - x_{2j}$ as the base and h_j the side. The base, $x_{1j} - x_{2j}$, is the distance between the two entities on the first axis, and h_j is the residual distance and lies perpendicular to the first axis. A residual distance, h_j, is calculated for every possible pair of entities and thus a residual distance matrix is created for each entity. The residual distances were used for selecting endpoints of the second axis and for the orthogonal projection of the remaining entities onto that axis. The methods of endpoint selection and orthogonal projection were the same as those used for the first axis. The third axis was similarly constructed from a new set of residual distance matrices derived from the second axis. This process can be repeated to give as many additional axes as desired. Each new axis is constructed from the residual distance matrices of the preceding axis. The methods of endpoint selection and axis construction used in this study have been described and rationalized by Beals and will be presented in a forthcoming publication (E.W. Beals, personal communication).

The coordinates for graphically positioning the entities in two or three dimensional space were derived from the axes used in the dimensional framework. When an entity is projected onto an axis, its distance from the base endpoint is its coordinate for that axis.

After the entity ordination was completed an ordination of the attributes (species) was made. Both ordinations were performed on a Univac 1110 using two programs, Bray and Curtis type ordination and graphic ordination plotting routine, graciously loaned to us by the University of Wisconsin Plant Ecology Laboratory.

RESULTS

Lutzomyia hartmanni, L. trapidoi, and *L. yuilli* accounted for 91% of the specimens taken in the series of forest night catches; *L. hartmanni, L. gomezi, L. yuilli,* and *W. rotundipennis* accounted for 89% of the specimens taken in the clearing series (Table 2). *L. hartmanni* dominated the man-biting activity in both habitats. *L. trapidoi* and *L. ayrozai* were distinctly sylvan whereas *L. gomezi* was taken primarily at the clearing sites. A complete list of the phlebotomine sand flies occurring in the Providencia region is presented as an appendix.

VERTICAL STRATIFICATION OF MAN-BITING ACTIVITY WITHIN THE FOREST

When the catches of the entire anthropophilic component at the three forest sites were combined, biting activity in the canopy was greater than at either of the other two levels (Table 3). The differences beween canopy and ground and between canopy and understory were declared to be highly significant by a nonparametric rank test (Tabel 4). However, the pattern of vertical stratification for the entire population varied considerably between the three sites (Tables 3 and 5). Between-site variation was greatest in the can-

Table 2. Summary of the common man-biting species taken during the night catches.[a]

	Forest			Clearing		
Species	No. of catch periods	No. taken	M_W[b]	No. of catch periods	No. taken	M_W
L. hartmanni	987	5422	2.60	432	1361	1.58
L. trapidoi	924	2109	0.91	432	77	0.10
L. yuilli	924	1204	0.54	432	227	0.20
L. panamensis	987	322[c]	0.13	432	133	0.15
L. ayrozai	987	141[c]	0.06	432	2	—[d]
L. bifoliata	987	104[c]	0.06	432	11	—
L. gomezi	987	95[c]	0.05	432	384	0.43
W. rotundipennis	987	88	0.05	432	219	0.27
Others[e]		127			23	

[a] Catch period 17 excluded.

[b] M_W is a modified geometric mean catch per period. See text for definition.

[c] The numbers taken for *L. panamensis*, *L. ayrosai*, *L. bifoliata*, and *L. gomezi* are actually somewhat larger for the forest habitat as 57 specimens belonging to these were not identified.

[d] M_W not computed as number taken was very small.

[e] Includes species taken in small numbers and the group of 57 specimens belonging to *L. panamensis*, *L. ayrozai*, *L. bifoliata*, and *L. gomezi*.

Table 3. Vertical stratification and total man-biting activity at the three forest sites for all species combined.

Site	**No. of catch periods**	**No. taken**	M_W[a]
Buenos Aires			
ground	119	1846	7.1
understory	119	841	3.4
canopy	119	1731	7.5
all levels	357	4418	5.7
Providencia			
ground	103	541	2.5
understory	103	686	3.4
canopy	103	2698	14.1
all levels	309	3925	5.2
Tiroteos			
ground	107	520	2.2
understory	107	626	3.3
canopy	107	533	2.6
all levels	321	1679	2.7
All Sites			
ground	329	2907	3.6
understory	329	2153	3.3
canopy	329	4962	6.7

[a] M_W is a modified geometric mean catch per period. See text for definition.

Table 4. Comparison of man-biting activity at three levels within the forest by means of a rank test. The three sites are combined.

		Rank totals			Standardized difference of rank totals (z)			
Species	Total no. of catch periods	Ground	Understory	Canopy	Standard error for a difference $(\sqrt{2n})^a$	Understory-Ground	Canopy-Ground	Canopy-Understory
All species	329	283.0	247.0	430.0	25.30	-1.42	5.81**	7.23**
L. hartmanni	329	299.5	260.5	364.0	24.82	-1.57	2.60*	4.17**
L. trapidoi	308	126.0	212.5	384.5	21.95	3.94**	11.78**	7.84**
L. yuilli	308	162.5	144.0	284.5	19.85	-0.93	6.15**	7.08**
L. panamensis	329	76.5	78.5	115.0	13.42	0.15	2.87*	2.72*

[a] The *n* does not correspond with the total number of catch periods because those periods in which all three levels had zero values were omitted.

* $P \leqslant 0.05$

** $P \leqslant 0.01$

opy and least in the understory where the modified geometric mean catch was remarkably similar at all three sites.

The vertical stratifications of man-biting activity for *L. hartmanni, L. trapidoi,* and *L. yuilli* are given for each of the forest sites in Tables 5 and 6 and are summarized for the three sites combined in (Tables 4 and 7). When the catches for the three forest sites were considered together, the activity of *L. hartmanni* was significantly ($P \leqslant 0.05$) greater in the canopy than at either of the other two levels. However, its vertical stratification varied between the individual sites. The man-biting activity of *L. trapidoi* was greatest in the canopy at all three sites: the only difference between the canopy and either of the other two levels that was not declared highly significant was that for understory at the Tiroteos site. When the catches of *L. yuilli* for the three forest sites were combined, activity in the canopy was significantly greater than that of either the ground or understory levels. At the Buenos Aires and Providencia sites, its vertical stratification was similar to that for the three sites combined, but at the Tiroteos site a significant difference was not detected between any of the levels.

If the patterns of vertical stratification of *L. hartmanni, L. trapidoi,* and *L. yuilli* (Table 5) are compared by site, differences in vertical stratification related to site may be distinguished from those due to species. Such comparisons revealed that the patterns of all three species were similar at the Providencia site but quite dissimilar at the Tiroteos site. At both the Buenos Aires and Providencia sites, biting activity of all three species was greater in the canopy than in the understory, and these differences were consistently highly significant ($P \leqslant 0.01$). At the Tiroteos site statistically significant difference between canopy and understory was detected only for *L. hartmanni,* and in this instante activity was greater in the understory. When activity in the canopy was compared with that on the ground, all three species had a highly significant preference for the canopy at the Providencia site. With the exception of *L. hartmanni,* this was also true for the Buenos Aires site. At the Tiroteos site only *L. trapidoi* was found to have a statistically significant preference for canopy over ground level. No significant difference was detected in the magnitudes of biting activity between understory and ground for any of the species at the Providencia site, and at the Buenos Aires site only *L. hartmanni* had a statistically significant preference; this, for the ground. At the Tiroteos site activity of *L. hartmanni* and *L. trapidoi* was significantly

Table 5. Comparison of the vertical stratification of man-biting activity at three forest sites by means of a rank test.

Species	Total no. of catch periods	Rank totals			Standar error for a difference ($\sqrt{2n}$)[a]	Standardized difference of rank totals (z)		
		Ground	Under-story	Canopy		Understory-Ground	Canopy-Ground	Canopy-Understory
All species								
Buenos Aires 1	119	141.0	60.5	152.5	15.36	-5.24**	0.75	5.99**
Providencia	103	56.5	67.5	179.0	14.21	0.77	8.62**	7.85**
Tiroteos	107	85.5	119.0	98.5	14.21	2.36*	0.91	-1.44
L. hartmanni								
Buenos Aires 1	119	152.5	65.5	133.0	15.30	-5.69**	1.27	4.41**
Providencia	103	59.0	74.5	157.5	13.93	1.11	7.07**	5.96**
Tiroteos	107	88.0	120.5	73.5	13.71	2.37*	-1.06	-3.43**
L. trapidoi								
Buenos Aires 1	106	58.5	57.0	130.5	12.81	-0.12	5.62**	5.74**
Providencia	95	34.5	58.5	147.0	12.65	1.90	8.89**	7.00**
Tiroteos	107	33.0	97.0	107.0	12.57	5.09**	5.89**	0.80
L yuilli								
Buenos Aires 1	106	72.5	57.0	119.5	12.88	-1.20	3.65**	4.85**
Providencia	95	36.0	35.5	120.5	11.31	-0.04	7.47**	7.52**
Tiroteos	107	54.0	51.5	44.5	10.00	-0.25	-0.95	-0.70
L. gomezi								
Providencia	103	28.0	27.5	88.5	9.80	-0.05	6.17**	6.22**
W. rotundipennis								
Providencia	103	40.0	35.5	38.5	8.72	-0.52	-0.17	0.34

[a] The *n* does not correspond with the total number of catch periods because those periods in which all three levels had zero values were omitted.

* $P \leqslant 0.05$

** $P \leqslant 0.01$

Table 6. Vertical stratification of man-biting activity by site for the common forest species.

	L. hartmanni			*L. trapidoi*			*L. yuilli*			*L. panamensis*		
Site	No. of catch periods	No. taken	M_W[a]	No. of catch periods	No. taken	M_W	No. of catch periods	No. taken	M_W	No. of catch periods	No. taken	M_W
Buenos Aires												
ground	119	1329	5.0	106	133	0.7	106	178	0.76	119	17	0.08
understory	119	472	2.0	106	132	0.7	106	122	0.57	119	9	0.05
canopy	119	898	4.2	106	420	1.9	106	269	1.42	119	42	0.15
Providencia												
ground	103	390	1.9	95	35	0.2	95	18	0.10	103	16	0.09
understory	103	465	2.6	95	113	0.6	95	12	0.08	103	32	0.11
canopy	103	1038	5.8	95	897	4.3	95	314	1.73	103	136	0.35
Tiroteos												
ground	107	270	1.3	107	29	0.2	107	145	0.36	107	17	0.09
understory	107	335	1.9	107	150	0.8	107	91	0.31	107	24	0.13
canopy	107	225	1.1	107	200	1.0	107	55	0.25	107	29	0.15

[a] M_W is a modified geometric mean catch per period. See text for definition.

greater in the understory than at ground level, but no significant difference between these levels was detected for *L. yuilli.*

The man-biting activity of *L. panamensis* for the three sites combined was significantly ($P \leqslant 0.05$) greater in the canopy than in the understory or on the ground. Like the three preceding species, the preference of *L. panamensis* for the canopy was most pronounced at the Providencia site (Table 6), but this preference was exaggerated by an abnormally large catch of 106 individuals in the canopy on July 7. With few exceptions *L. ayrozai* was confined to ground level, while most *L. bifoliata* were taken in the canopy (Table 7). The latter species' preference was more marked at the Providencia site than at the Tiroteos site. The vertical stratifications observed for *L. gomezi* and *W. rotundipennis* are based only on catches at the Providencia site as they were seldom encountered at the other forest sites. While *L. gomezi* was taken primarily in the canopy, a statiscally significant preference between levels was not detected for *W. rotundipennis.*

The little diurnal man-biting activity that occurred was primarily by *L. trapidoi* in the understory and by *L. panamensis* on the forest floor (Table 14).

VARIATION IN MAN-BITING ACTIVITY BETWEEN THE FOREST SITES

The modified geometric mean catch for all species combined was only about one-half as large for the Tiroteos site as it was for each of the other two sites (Table 3). An analysis of total biting activity during the first seven catch periods indicated that the F ratios for sites, levels, and the sites times levels interaction were all significant at the 1% level (Table 9). Thus, there is evidence of both a systematic difference in biting activity between sites regardless of level and of a difference in biting activity between sites dependent upon level. A statistically significant contrast (Table 10) between a pair of sites for all levels combined suggests that there is a systematic difference between the two sites over the three levels, although it may also result from the accumulative effect of two contrasts with large values in the same direction. The highly significant ($P \leqslant 0.01$) Scheffé contrast between the Buenos Aires and Tiroteos sites for the composite population appeared to be due primarily to the relatively large positive contrasts for the ground and canopy. A highly significant interaction in

Table 7. Vertical stratification of man-biting activity of the common forest species. The three forest sites are combined.

Species	No. of catch periods	No. taken	M_W[a]	No. of catch periods	No. taken	M_W
	L. hartmanni			*L. ayrozai*		
ground	329	1989	2.50	329	135	0.16
understory	329	1272	2.16	329	4	0.01
canopy	329	2161	3.23	329	2	0.00
	L. trapidoi			*L. bifoliata*		
ground	308	197	0.36	329	11	0.02
understory	308	395	0.68	329	22	0.04
canopy	308	1517	2.07	329	71	0.12
	L. yuilli			*L. gomezi*[b]		
ground	308	341	0.39	103	7	0.04
understory	308	225	0.31	103	4	0.03
canopy	308	638	1.00	103	83	0.52
	L. panamensis			*W. rotundipennis*[b]		
ground	329	50	0.09	103	37	0.18
understory	329	65	0.09	103	21	0.14
canopy	329	207	0.21	103	26	0.16

[a] M_W is a modified geometric mean catch per period. See text for definition.
[b] Values from Providencia forest site only.

the analysis of variance may be reflected in the Scheffé contrasts. Thus, the contrasts for all levels combined would tend to be statistically not significant, whereas the corresponding contrasts for the individual levels would tend to be statistically significant in opposite directions. For example, consider the contrasts between the Buenos Aires and Providencia sites for the composite population. A significant contrast was not detected for the three levels combined; however, the contrasts of the individual levels varied considerably in magnitude. Thus, while biting activity was significantly greater on the ground at the Buenos Aires site, there is an indication that it was somewhat greater in the canopy at the Providencia site.

The man-biting activity of the common forest species is summarized for each of the forest sites in Table 11. The modified geomet-

Table 8. Vertical stratification of diurnal man-biting activity.

	Ground[a]	Understory	Canopy
L. bifoliata	2	1	-[b]
L. gomezi	1	1	2
L. hartmanni	4	2	1
L. olmeca bicolor	1	-	-
L. panamensis	10	5	-
L. ayrozai	-	1	-
L. trapidoi	5	14	1
L. yuilli	1	4	1
W. rotundipennis	-	-	1

[a] 592 catch periods per level.
[b] A dash indicates that no specimens were encountered.

Table 9. Analyses of variance of the forest catches for all species combined and the three most abundant species[a]

Source:	d.f.[b]	m.s.	F	s.p.	d.f.	m.s.	F	s.p.
	—All species —				*L. trapidoi*			
Corrected total	104				95			
Site	2	6.844370	7.29	.0011	2	2.813150	2.93	.0588
Level	2	6.593508	7.02	.0014	2	26.332536	27.41	.0000
Site x level	4	3.828921	4.08	.0043	4	5.005200	5.21	.0008
Variation within cells	96	.938703			87	.960582		
	L. hartmanni				*L. yuilli*			
Corrected total	104				95			
Site	2	9.955906	11.03	.0000	2	11.346812	13.67	.0000
Level	2	2.024240	2.24	.1118	2	14.631241	17.63	.0000
Site x level	4	2.554633	2.83	.0288	4	6.668001	8.04	.0000
Variation within cells	96	.902918			87	.829811		

[a] Based on the first seven night catch periods.

[b] d.f. = degrees of freedom; m.s. = mean square; F = variance ratio; s.p. = significance probability.

ric mean catches of *L. hartmanni* for the Buenos Aires and Providencia sites were more than twice the mean catch for the Tiroteos site. In the analysis of variance for this species, the F ratio for sites was highly significant, and the sites times levels interaction was statistically significant at the 5% level (Table 9). The significant difference detected for sites can be primarily attributed to a greater magnitude of biting activity at all three levels at the Buenos Aires site than at the Tiroteos site (Table 10). The significant interaction is perhaps best reflected in the large variation in the size of the contrasts between the Buenos Aires and Providencia sites. Although the modified geometric mean catch of *L. trapidoi* at the Providencia site was nearly twice as large as that at the Tiroteos site, the F ratio for sites was not quite significant at the 5% level. Also, none of the pairwise contrasts for all levels combined was declared to be statistically significant. The sites times levels interaction for *L. trapidoi* was very highly significant ($P \leqslant 0.0001$) and this is reflected in the pairwise contrast for the individual levels between the Buenos Aires and Providencia sites and between the Providencia and Tiroteos sites. The geometric mean catch for *L. yuilli* at the Buenos Aires site was nearly three times as large as that at the Tiroteos site. The F ratios from the analysis of variance for sites, levels, and the interaction were all very highly significant ($P \leqslant 0.001$). The two highly significant contrasts for all levels combined reflect the greater amount of biting activity by *L. yuilli* at Buenos Aires than at either of the other sites. The contrasts between the Providencia and Tiroteos sites for ground and understory are quite similar and differ markedly from the contrast for the canopy.

When the pairwise contrasts in Table 10 are considered for all three species, some differences in biting activity related to site can be observed. The contrasts for all levels combined suggest that biting activities of *L. hartmanni* and *L. yuilli* were greater at Buenos Aires than at either of the other two sites. Also, for all levels combined, there were no statistically significant differences between the Providencia and Tiroteos sites for any of the three species. This indicates that none of these species had a distinct preference at all three levels for either site. With one exception, the biting activites of all three species at ground level were significantly greater at Buenos Aires than at either of the other two sites. As noted earlier, in the understory the magnitude of biting activity of each species was quite similar at all three sites. In the canopy the biting activities of all three species

Table 10. Pairwise contrasts of man-biting activity between three forest sites using Scheffé's multiple comparison method.

Species	Ground			Understory			Canopy			All levels		
	BA[a]vsP	BAvsT	PvsT	BAvsP	BAvst	PvsT	BAvsP	BAvsT	PvsT	BAvsP	BAvsT	PvsT
All species	3.604**	3.223*	-0.269	1.094	0.750	-0.298	-1.104	2.702	3.578**	2.076	3.855**	1.739
L. hartmanni	3.597**	4.140**	0.607	0.951	1.149	0.212	-0.306	2.925*	3.054*	2.447	4.741**	2.236
L. trapidoi	3.393*	3.302*	-0.087	0.893	-0.820	-1.640	-1.422	1.672	2.963*	1.655	2.397	0.711
L. yuilli	3.653**	1.792	-1.782	3.184*	1.684	-1.436	-0.062	5.291**	5.125**	3.912**	5.062**	1.101

[a] BA = Buenos Aires 1, P = Providencia, T = Tiroteos.
* $P \leq 0.05$
** $P < 0.01$

Table 11. Summary of man-biting activity by species at the three forest sites.

Site	No. of catch periods	No. taken	M_W[a]	No. of catch periods	No. taken	M_W
		L. hartmanni			*L. panamensis*	
Buenos Aires	357	2699	3.57	357	68	0.09
Providencia	309	1893	3.13	309	184	0.18
Tiroteos	321	830	1.42	321	70	0.12
		L. trapidoi			*L. ayrozay*	
Buenos Aires	318	685	1.04	357	92	0.12
Providencia	285	1045	1.16	309	4	0.01
Tiroteos	321	379	0.61	321	45	0.03
		L. yuilli			*L. bifoliata*	
Buenos Aires	318	569	0.88	357	9	0.02
Providencia	285	344	0.48	309	59	0.10
Tiroteos	321	291	0.30	321	36	0.07

[a] M_W is a modified geometric mean catch per period. See text for definition.

were declared to be significantly greater at the Providencia site than at the Tiroteos site, but no statistically significant differences were detected between the Providencia and Buenos Aires sites.

The total number of individuals of some of the less abundant species taken in the forest catches is given by site in Table 11. *L. panamensis* was taken most frequently at the Providencia site where the modified geometric mean catch was twice as large as that for the Buenos Aires site. *L. ayrozai* was most abundant at Buenos Aires and was rarely taken at the Providencia site. *L. bifoliata* was most frequently taken at the Providencia and Tiroteos sites. Man-biting activity by *L. gomezi* (94 of 95 individuals) and *W. rotundipennis* (84 of 88 individuals) was almost entirely confined to the Providencia site.

VARIATION IN MAN-BITING ACTIVITY BETWEEN THE CLEARING SITES

Abundance comparisons. There was considerable variation in the magnitude of man-biting activity between the six clearing sites (Table 12). Larger numbers were taken

Table 12. Total man-biting activity at the six clearing sites for all species combined.

Site	No. of catch periods	No. taken	M_W[a]
A	72	97	0.8
B	72	259	2.0
C	72	218	1.7
D	72	574	3.9
E	72	821	6.9
F	72	468	2.6

[a] M_W is a modified geometric mean catch per period. See text for definition.

at the two forest-clearing margin sites, D and E, than at sites located within the clearing, i.e., A,B,C, and F. The smallest number of specimens was obtained from site A which was adjacent to the Río Anorí and farthest from relatively mature forest.

The man-biting species most frequently taken in the clearing catches and the percent of the catch attributed to each are as follows: *L. hartmanni,* 56%; *L. gomezi,* 16%; *L. yuilli,* 9%; *W. rotundipennis,* 9%; *L. panamensis,* 5%; and *L. trapidoi,* 3%. The man-biting activity of these species is summarized for each site in Table 13. *L. hartmanni* was the most abundant species at all six of the clearing sites, although *L. gomezi* was almost as numerous at site C. A highly significant difference in biting activity between the clearing sites was detected for *L. hartmanni, L. gomezi, L. yuilli, L. trapidoi,* and all species combined (Table 14). For each of these species and the composite population, a comparison was made by means of a Scheffé contrast beween the two forest-clearing margin sites and the four sites within the clearing. The comparison for *L. gomezi* was the

Table 13. Summary of man-biting activity at the six clearing sites by the more abundant species.

Site[a]	No. taken	M_W[b]	No. taken	M_W
	L. hartmanni		*L. trapidoi*	
A	75	0.61	3	0.03
B	186	1.45	2	0.02
C	82	0.72	1	0.01
D	349	2.44	19	0.17
E	439	4.00	36	0.31
F	230	1.50	16	0.11
	L. gomezi		*L. yuilli*	
A	7	0.07	2	0.02
B	35	0.29	0	0.00
C	80	0.59	13	0.09
D	22	0.17	43	0.32
E	154	1.06	123	0.63
F	86	0.63	46	0.25
	L. panamensis		*W. rotundipennis*	
A	2	0.02	8	0.06
B	6	0.06	28	0.21
C	7	0.07	33	0.29
D	74	0.41	63	0.43
E	30	0.28	27	0.24
F	14	0.12	60	0.40

[a] 72 catch periods per site.

[b] M_W is a modified geometric mean catch per period. See text for definition.

Table 14. Comparisons of man-biting activity between the six clearing sites using Scheffé's multiple comparison method.

Species	F for sites	*t* ratios for simple differences									Analysis for the contrast D + E vs A + B + C + F		Transformation
		AvsC[a]	AvsD	AvsE	AvsF	BvsD	BvsE	CvsD	CvsE	DvsE	t ratio	95% confidence interval using Scheffé	
All species	8.42**	-[b]	4.69**	5.66**	3.70*	-	-	-	3.77*	-	5.21**	1.46 to 7.95	$\log_e(x + 1.0)$[c]
L. hartmanni	7.35**	-	3.88*	4.57**	-	-	-	3.94*	4.63**	-	5.19**	1.48 to 8.71	$\log_e(x + 1.0)$
L. gomezi	8.98**	4.23*	-	5.44**	4.35**	-	-	-	-	4.44**	0.73		$\log_e(x + 1.0)$
W. rotundipennis	1.66	-	-	-	-	-	-	-	-	-			$\log_e(x + 1.0)$
L. panamensis	1.86	-	-	-	-	-	-	-	-	-			$\log_e(x + 0.1)$
L. yuilli	8.85**	-	-	4.40**	-	4.26*	5.40**	-	3.91*	-	5.41**	2.42 to 84.44	$\log_e(x + 0.1)$
L. trapidoi	5.35**	-	-	-	-	-	-	-	4.07*	-	4.97**	1.97 to 71.24	$\log_e(x + 0.1)$

[a] None of the following single comparisons gave rise to a statistically significant t value and thus have been omitted from the table:
A vs B, B vs C, B vs F, C vs F, D vs F, E vs F.

[b] A dash indicates a nonsignificant ratio for simple differences.

[c] x is the total catch of a species for a given night and site.

* $P \leq 0.05$

** $P \leq 0.01$

only one which was not declared to be statistically significant. The 95% confidence intervals associated with the statistically significant multiple comparisons indicate that the biting activities of *L. hartmanni, L. yuilli, L. trapidoi,* and the composite population were greater at the two forest margin sites. The confidence intervals for *L. yuilli* and *L. trapidoi* are very large, but they do indicate that the biting activities of these two species were respectively, at least 2.4 and 2.0 times greater at the forest-clearing margin than within the clearing.

When comparisons of biting activity were made between individual sites (Table 14), statistically significant differences were detected most frequently between sites A and E and between C and E. The pairwise comparisons declared to be statistically significant for *L. hartmanni, L. yuilli,* and *L. trapidoi* were always between a forest margin site and one of the sites within the clearing. *L. gomezi* was the only species for which statistically significant differences were detected between sites within the clearing, i.e., between A and C and between A and F, and between the two forest-clearing margin sites, D and E. Since a statistically significant difference in biting activity between the six clearing sites was not detected for *W. rotundipennis* and *L. panamensis,* the multiple and pairwise comparisons were not computed for these species.

For each species listed in Table 13 the pattern of its biting activity for the six clearing sites was compared with the pattern of each of the other species, and estimates of their similarity are given in Table 15 as F ratios for interaction between species and sites. The main effect F ratio (F for relative abundance) for each comparison was used as a test of significance for comparing the relative abundance, i.e., as measured by biting activity, of the two species. Statistically significant differences were detected between the biting pattern of *L. gomezi* for the clearing sites and the patterns of all of the other species except *W. rotundipennis.* When the magnitude of the biting activity of *L. gomezi* was compared with that of the other species, a significant difference was detected for all comparisons except that with *W. rotundipennis.* Thus, *L. gomezi* and *W. rotundipennis* were similar in both pattern of biting activity across the six sites and in abundance. The most apparent difference between the two species was in the magnitude of their activity at the two forest-clearing margin sites. A single confidence interval for the abundance ratio was calculated, as the interaction between these two species and sites was not statistically significant. Thus, for any one of the six sites, *L. gomezi* was estimated to be between 0.85 and 2.7 times as abundant as *W. rotundipennis.*

A statistically significant difference between the patterns of biting activity of two species for the clearing sites indicates that the ratios of their biting activity vary significantly between some of the sites. In these instances separate confidence intervals were constructed for each of the sites. For example, the F ratio for interaction between species and sites for the comparison of *L. hartmanni* and *L. gomezi* was declared to be highly significant. Inspection of the confidence intervals for individual sites reveals a range in the lower limits from 0.6 at site C to 10.7 at site D.

A significant difference was not detected between the pattern of biting activity of *L. panamensis* for the clearing sites and those of any of the other species except *L. gomezi.* Significant differences were not detected for comparisons between *L. panamensis, L. yuilli,* and *L. trapidoi* for either their biting patterns across the clearing sites or their relative abundances. As already shown *L. hartmanni* was the most numerous species in the clearing catches. When the magnitude of its biting activity was compared with that of each of the other species, the differences were consistently found to be highly significant ($P \leqslant 0.01$).

Diversity and evenness of Phlebotominae man-biting activity. The lowest values of diversity and evenness were associated with the two sites farthest from mature forest, i.e., sites A and B (Table 16). The estimates of diversity for the two edge sites, D and E, were slightly less than that for site F at the margin of pioneer vegetation but similar to that for site C within the pasture. The estimates of evenness or equitability for the two edge sites were equal and intermediate between the low values for sites A and B and the higher values for the two most exposed sites, C and F.

DIFFERENTIATION OF MICROENVIRONMENTS AND SPECIES ON THE BASIS OF THE MAN-BITING CATCHES.

The first three axes of the ordination of the 132 night catches in eight dimensional species space are presented in Figs. 7 and 8. An ordination of the eight species in the space of the catches is given in Fig. 9. The latter provides a visual expression of the similarity of these species as indicated by certain aspects of their man-biting activity.

Microenvironment ordination. The ordination of the catches as points in species space is considered first. Fig. 7 shows that the first axis separated the forest canopy catches (right end of the axis) from those taken within the clearing (left end of the axis). The catches for ground level at all three forest sites, for the understory at the Providencia site, and for the two edge sites, D and E, tend to be concentrated at the center of the axis. The canopy catches were dominated by *L. hartmanni, L. trapidoi,* and *L. yuilli.* The

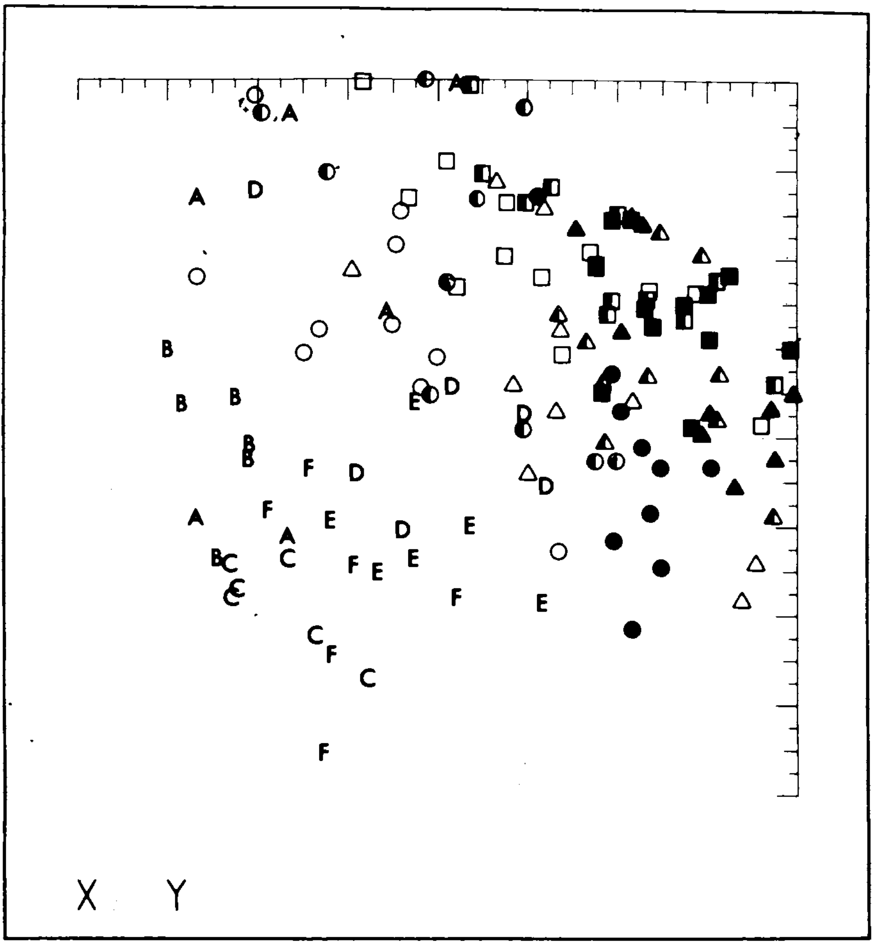

Fig. 7. The first two axes of the ordination of the forest and clearing night catches. The first ordination axis is the abscissa and the second is the ordinate. Key to symbols in Figs. 7 and 8: A-F = clearing sites, square = Buenos Aires 1 forest site, circle = Providencia forest site, triangle = Tiroteos forest site, open symbols = ground, half open = understory, closed = canopy.

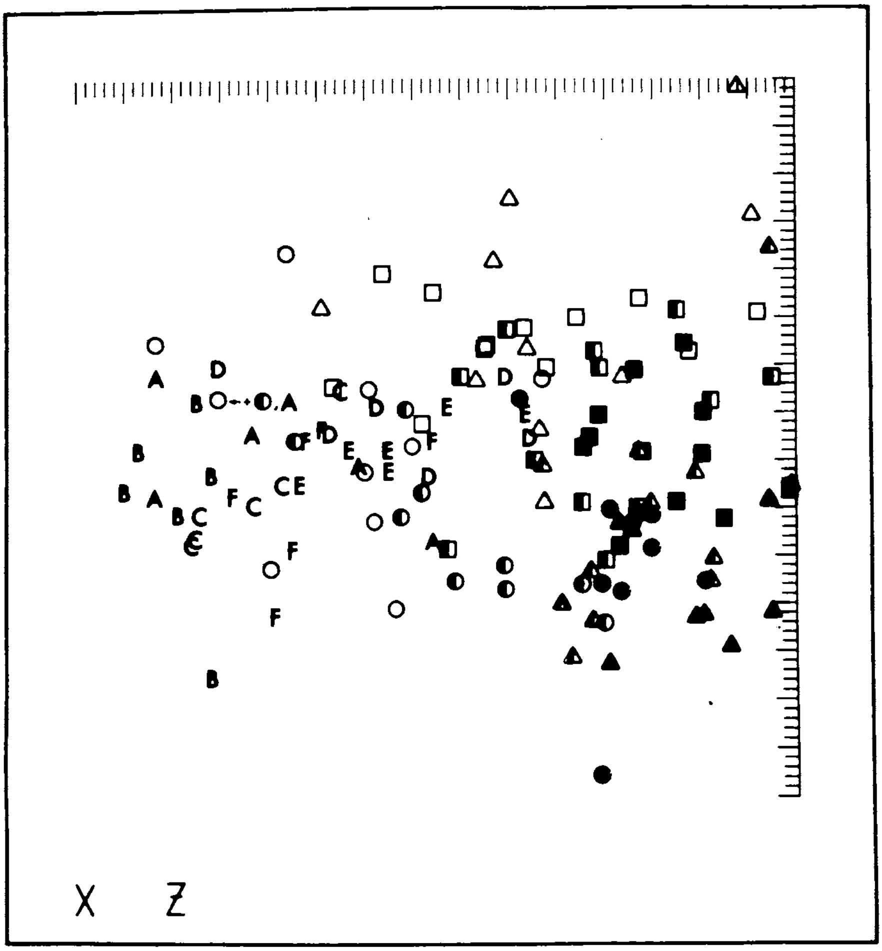

Fig. 8. The first and third axes of the ordination of the forest and clearing night catches. The first ordination axis is the abscissa and the third is the ordinate. For key to symbols, see legend to Fig. 7.

presence of both *L. trapidoi* and *L. yuilli*, with one or both occurring in relatively large numbers, and an absence of *L. ayrozai* tended to be characteristic of the canopy catches. The biting activity of *L. yuilli* and/or *L. trapidoi* was similar in magnitude to that of *L. hartmanni* in the catches at the extreme right-hand end of the axis. *L. panamensis* was frequently present in the canopy catches in small numbers. *L. hartmanni* was ubiquitous, occurring in all 132 of the catches. The catches for clearing sites B, C, and A, which are positioned at the left-hand end of the first axis, were characterized by an absence of *L. trapidoi*, *L. yuilli*, *L. ayrozai*, and *L. bifoliata*. Both *L. gomezi* and *W. rotundipennis* were present in nearly all these catches, although the latter species usually occurred in small numbers. *L. panamensis* was present in about half of the catches. Although *L. trapidoi* and usually *L. yuilli* were present in the catches near the center of the first axis, they tended to occur at a magnitude much less than that of *L. hartmanni*.

The second axis (Fig. 7) separated many of the ground and understory catches at the Buenos Aires site and understory catches at the Providencia site (upper end of the axis) from the catches at clearing sites C, F, and E and some of the canopy catches at the Provi-

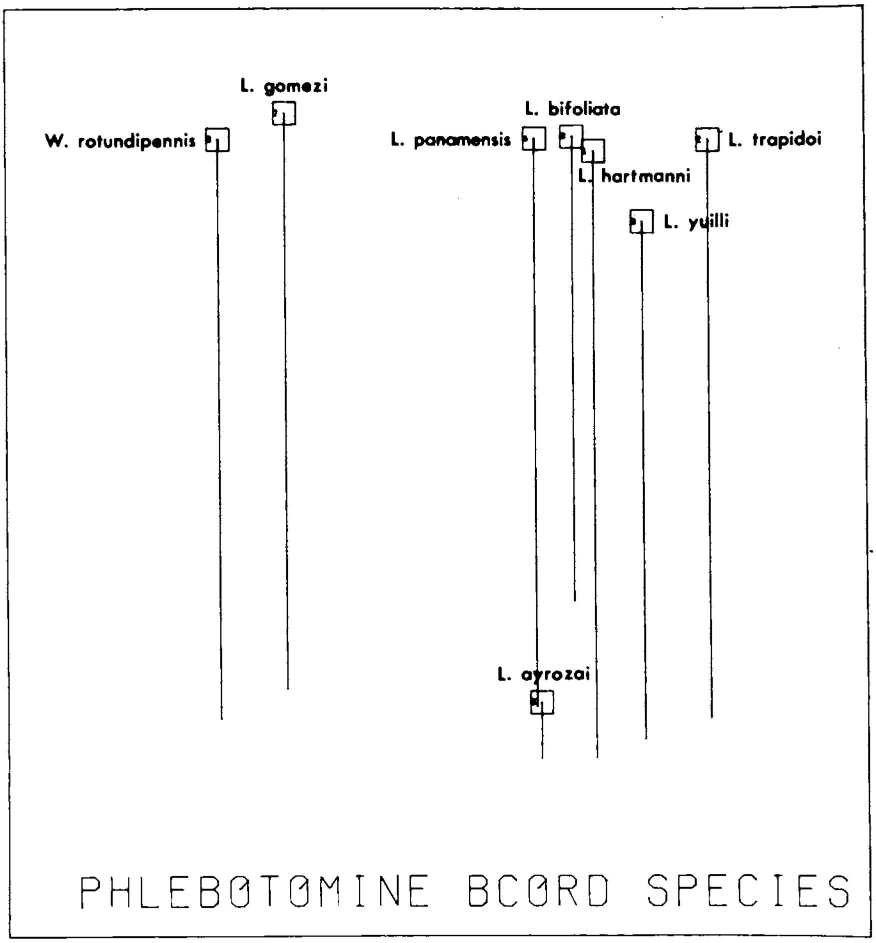

Fig. 9. A scatter diagram of the species taken most frequently in the man-biting catches. The species are in the space of the first three ordination axes. The squares may be considered as the heads of pins which are standing on the inclined plane of the first and third ordination axes. The horizontal axis represents the first ordination axis. The length of the pins indicate their position on the second axis.

dencia site (lower end of the axis). The understory and ground level catches near the upper end point were dominated by *L. hartmanni* and rarely contained any other species except *L. trapidoi* which was also occasionally absent. The catches somewhat below the end point tended to have, in addition, small numbers of *L. yuilli* and occasionally another species. At the opposite end of this axis, species diversity became considerably greater. *L. gomezi, W. rotundipennis, L. panamensis* and *L. yuilli* were nearly always present and the combined total of these species exceeded that of *L. hartmanni.*

Together, the first two axes have quite distinctly differentiated clearing sites B, C, E, and F from the forest sites (Fig. 7). The catches at clearing sites A and D tend to be associated with those for the ground and understory levels at the Providencia site and with those for the forest floor at the Tiroteos site. The canopy and understory catches at Buenos Aires are clustered in the upper right-hand corner of the ordination and were composed almost exclusively of *L. hartmanni, L. trapidoi,* and *L. yuilli. L. trapidoi* tended to be quite numerous in these catches but was somewhat less abundant than *L.*

hartmanni. The canopy catches at the Providencia site are positioned directly below those for the Buenos Aires canopy and understory. The Providencia canopy catches were primarily distinguished from the latter by having a greater number of species. In addition to the three species taken at the Buenos Aires site, *L. gomezi, L. bifoliata, W. rotundipennis,* and *L. panamensis* were present in nearly all of these catches. Many of the forest ground level catches are positioned to the left of the Buenos Aires canopy and understory catches. These ground level catches differed from the latter by having a higher percentage of *L. hartmanni* relative to *L. trapidoi* and by the presence of one or two additional species. *L. ayrozai* usually occurred in the ground level catches at Buenos Aires and *W. rotundipennis* was regularly taken on the forest floor at the Providencia site. *L. panamensis* was present in half of the ground level catches. The catches for clearing sites B, C, E and F are the furthest away from the Buenos Aires canopy and understory catches and thus are the most dissimilar. *W. rotundipennis* and *L. gomezi* were consistently present in these catches, but with the exception of site E, *L. trapidoi and L. yuilli* were usually absent. *L. panamensis* was also frequently present. The catches for these clearing sites form groups which partially overlap from site B at the extreme left to site E at the lower center of the ordination.

The third axis, the Z axis in Fig. 8, separated the ground level catches at the Buenos Aires and Tiroteos sites and a number of Buenos Aires understory catches (upper end of the axis) from many of the canopy and understory catches at the Tiroteos and Providencia sites (lower end of the axis). The catches near the upper end point tended to have *L. yuilli* present in larger numbers than *L. trapidoi. L. ayrozai* was frequently present and occured in relatively large numbers in the few instances where *L. trapidoi* was more abundant than *L. yuilli.* Although *L. bifoliata* was absent from the catches at the upper end of the Z axis, it was nearly always present in the catches at the lower end. The catches near the lower end point characteristically had *L. trapidoi* more abundant than *L. yuilli* and consistently lacked *L. ayrozai. L. panamensis* occurred in a uniform proportion of the catches along the entire length of the Z axis.

Species ordination. The first three axes of the ordination of the eight species as points in the space of the catches are given in Fig. 9. *W. rotundipennis* and *L. gomezi* are clearly separated from the other species on the first axis. Both species were present in nearly all clearing catches but, with few exceptions, were taken in the forest catches only at the Providencia site. These two species differed from each other in their biting activity at the two edge sites, D and E, and in their pattern of vertical stratification at the Providencia forest site. Although not considered by the ordination, they also differed in their diel pattern of biting. The second axis distinctly separated *L. ayrozai,* wich, unlike the other species, was taken almost exclusively at ground level. *L. ayrozai* was encountered primarily at the Buenos Aires and Tiroteos sites and was rarely taken in the clearing catches. The third axis distinguished *L. bifoliata,* a species which was taken rather infrequently and whose biting activity tended to be concentrated in the canopy of the Providencia site and the canopy and understory of the Tiroteos site.

Although Fig. 9 suggests that *L. hartmanni, L. panamensis, L. yuilli, L. trapidoi,* and *L. bifoliata* were rather similar in their biting activity, some aspects such as diel periodicity were not considered in the ordination. Some of the more apparent similarities and differences in the man-biting activity of these five species have been described above and form the basis of the following comparisons. The biting activity of each species varied in magnitude between the three forest sites (Table 11). In some instances the between-site differences were statistically significant (Table 10). *L. hartmanni* and *L. yuilli* had rather similar ratios of activity between the three forest sites: both were taken in substantially greater numbers at the Buenos Aires site than at either of the other two locations. *L. bifoliata,* however, was seldom encountered at Buenos Aires and occurred in greatest numbers at the Providencia site. *L. trapidoi* and *L. panamensis* were also most numerous at the Providencia site. When summarized over sites, the biting activity of each of the five species was greater in the canopy than in the understory or on the forest floor. However, the proportion of the catch occurring in the canopy varied considerably between species and was greatest for *L. bifoliata* and *L. trapidoi.* Statistically significant differences were detected between the clearing sites for *L. hartmanni, L. trapidoi,* and *L. yuilli.* The biting activity of each was significantly greater at the two edge sites, D and E, than at the sites within the clearing. Although *L. panamensis* was also taken in greater numbers at the two forest-clearing margin sites than at the sites within the clearing, a statistically significant difference was not detected. *L. bifoliata* was seldom encountered in the clearing catches. The magnitude of biting activity between the forest and clearing habitats was either relatively similar as for *L. panamensis* and *L. hartmanni* or decidedly greater at the forest sites. With the exception of *L. panamensis,* these species did not appear to have large seasonal fluctuations in biting activity.

Neither the habitat nor the species ordinations appear to have been discernibly influenced by seasonality, although this may be due to the relatively small sample size.

SUMMARIZATION OF THE TEMPORAL PATTERNS OF MAN-BITING ACTIVITY IN THE FOREST AND CLEARING HABITATS

The summary temporal patterns of nocturnal man-biting activity for the entire population and for *L. hartmanni, L. trapidoi, L. yuilli,* and *L. panamensis* are presented in Figs. 10 to 14 for both the forest and clearing habitats. The number of specimens obtained and the modified geometric mean catch per period are given in Tables 17 to 19. The daytime catch periods were not included in the graphs because diurnal biting by phleboto-

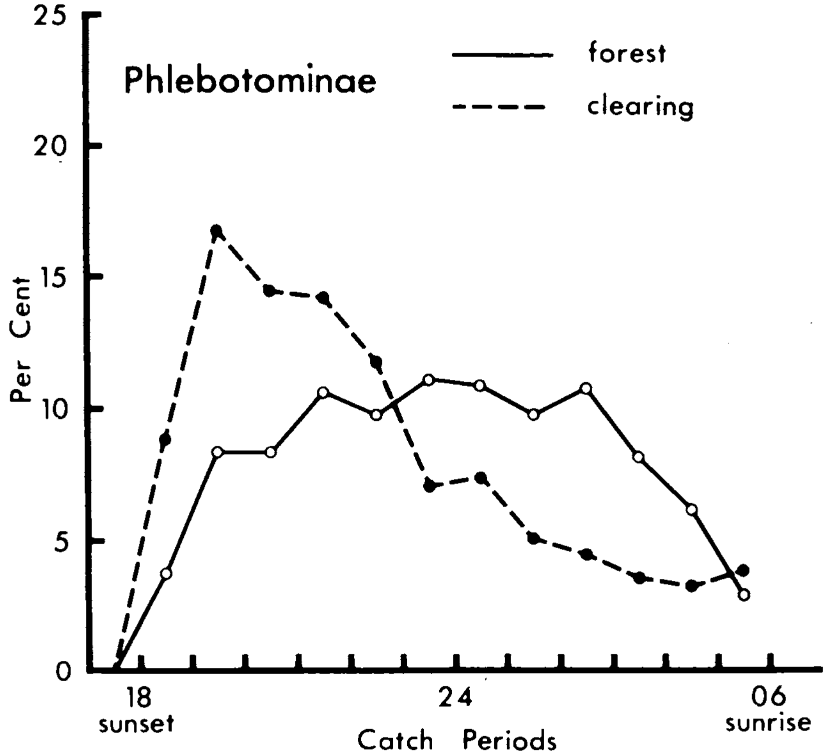

Fig. 10. Summary temporal patterns of man-biting activity in forest and clearing habitats by all species combined based on modified geometric means converted to percentages. Each catch period approximates the corresponding hour as described in the text.

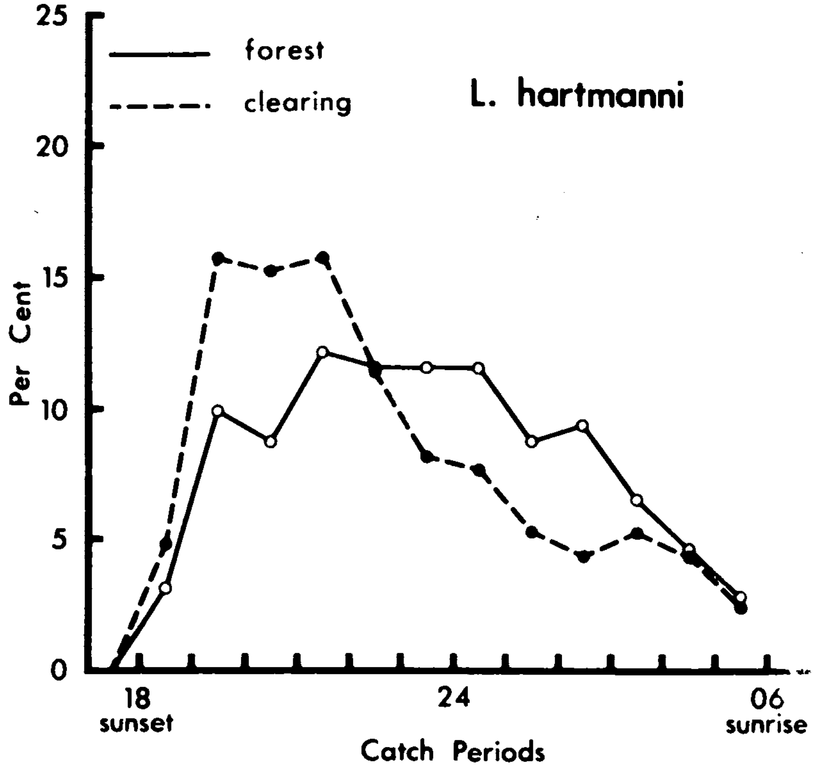

Fig. 11. Summary temporal patterns of man-biting activity in forest and clearing habitats by *L. hartmanni* based on modified geometric means converted to percentages. Each catch period approximates the corresponding hour as described in the text.

mine sand flies was infrequent (Table 20) in the Providencia study area.

Within the forest there were extensive variations between nights in the temporal pattern of the man-biting actvity of *L. hartmanni* (Fig. 15). There were variations in both time of maximum biting activity and in the shape of the nightly temporal patterns. In Fig. 16 the nightly temporal patterns presented in Fig. 15 are partitioned by vertical level. On most of these nights, there tended to be sharp peaks in biting activity at two or all three of the levels. These peaks appeared to be somewhat synchronized, usually occurring within one or two catch periods of each other. There is no indication that the biting activity of *L. hartmanni* consistently reached a peak earlier at one level than at either of the other two. A summarization by level of the nightly temporal patterns of the biting activity of *L. hartmanni* is not presented since an averaging of such highly variable biting activity would tend to distort its true nature.

There was also a considerable amount of between-night variation in the temporal biting pattern of *L. hartmanni* for the clearing catches (Fig. 17). The extent of between-night differences in the temporal biting pattern at each clearing site appeared to be partially related to the site, e.g., the temporal pattern at site E was quite variable while at site D it was relatively uniform. Most of the catches at sites A, B, C, and F contained an insufficient number of individuals to be meaningfully graphed. The modified geometric mean catches for periods 18 through 21 were similar between the forest and clearing habitats but became substantially reduced in the latter after 2100 hours.

The biting activity of *L. trapidoi* also tended to be concentrated earlier in the clearing than in the forest habitat (Fig. 12). How-

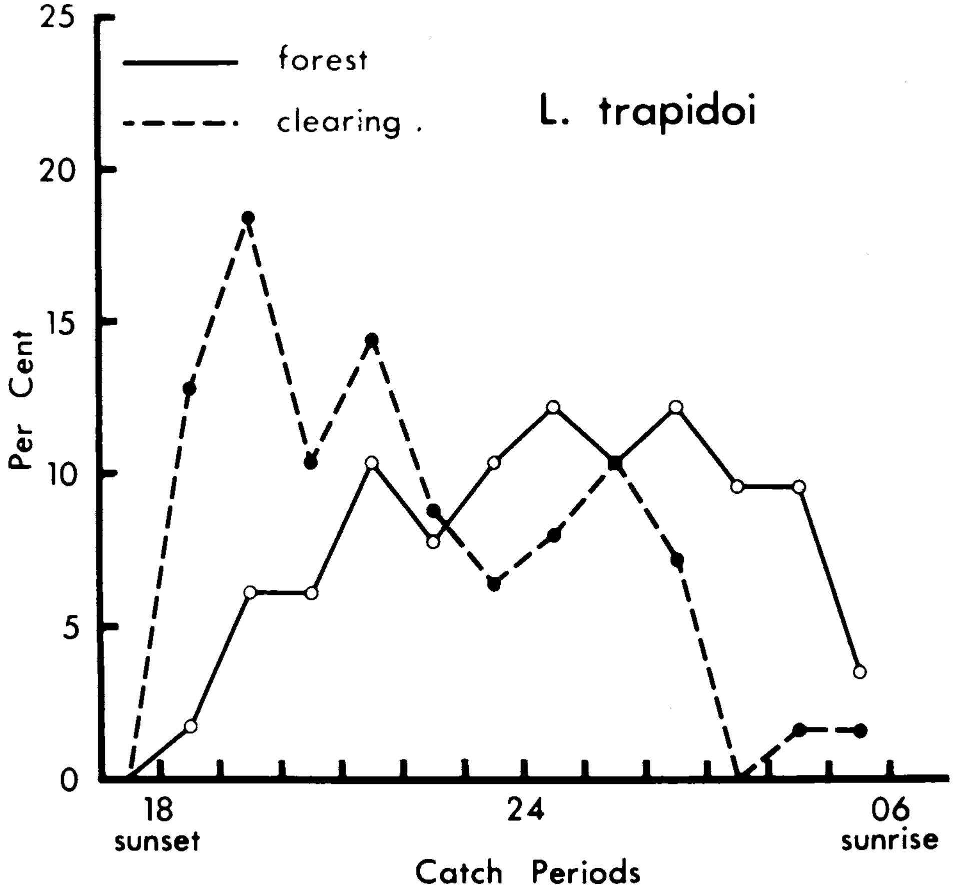

Fig. 12. Summary temporal patterns of man-biting activity in forest and clearing habitats by *L. trapidoi* based on modified geometric means converted to percentages. Each catch period approximates the corresponding hour as described in the text.

ever, the modified geometric mean of each catch period was consistently larger for the forest than the clearing habitat. The biting activity of *L. trapidoi* at the clearing sites occurred at such a low magnitude (Table 2) that further meaningful observations concerning the temporal pattern of its biting activity in this habitat cannot be made. Fig. 18 indicates that within the forest there was considerable variation between nights in the temporal patten of biting activity and that prominent peaks in biting activity occurred on a number of the nights. Figs. 12 and 19 thus present a distortion of the nightly temporal patterns of biting activity which were frequently in the form of a transient wave. However, Table 21 and Fig. 19 do indicate that the biting activity of *L. trapidoi* at the ground and understory levels was not concentrated in a limited portion of the night. An examination of the catches for individual nights indicated that there frequently was some synchronization of biting activity between the three vertical levels; however, there was no evidence that the biting activity of this species tended to reach a peak at one level before reaching a peak at another. Fig. 19 also reveals that very little biting activity occurred at ground level during the first three catch periods after sunset. Although sample size was insufficient to determine the extent of between-site variation in the temporal patterns of biting activity no striking differences were apparent.

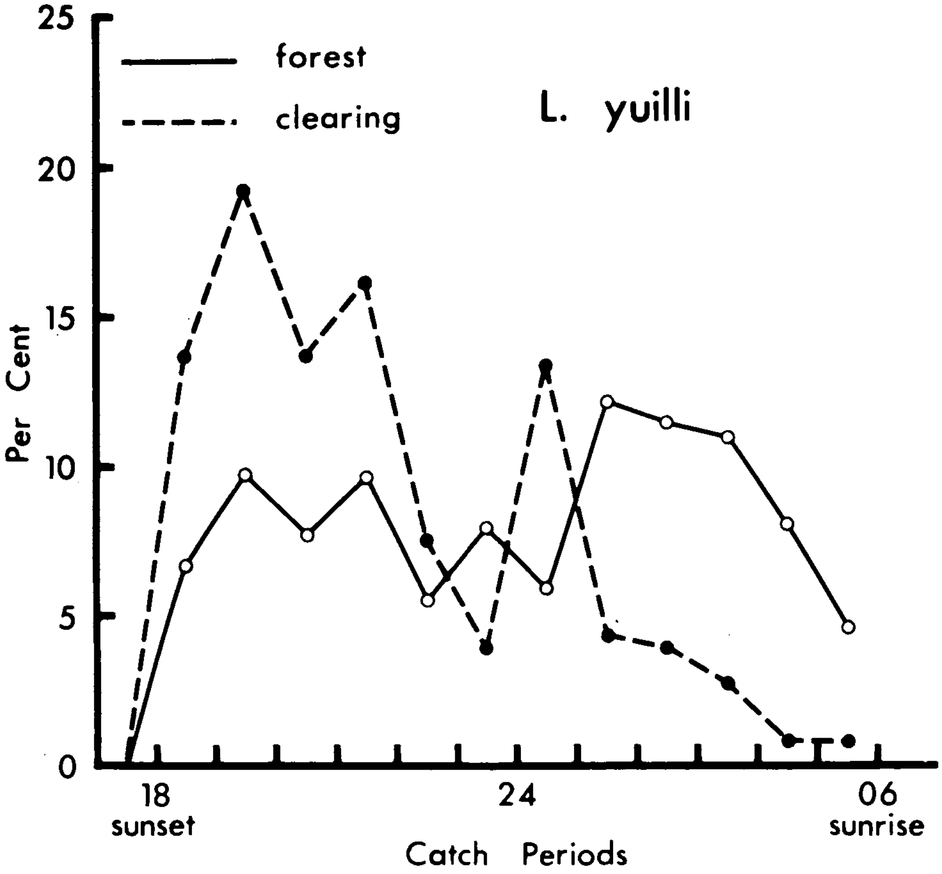

Fig. 13. Summary temporal patterns of man-biting activity in forest and clearing habitats by *L. yuilli* based on modified geometric means converted to percentages. Each catch period approximates the corresponding hour as described in the text.

The man-biting activity of *L. yuilli* tended to be concentrated somewhat earlier in the clearing than in the forest habitat (Fig. 13). As with *L. trapidoi,* the modified geometric mean of each catch period was larger for the forest than the clearing habitat (Tables 18 and 19). Again, the summary tempo ral patterns (Fig. 13) distorted the nature of the nightly biting activity. The temporal pattern of *L. yuilli* for the forest catches was quite variable from one night to another (Fig. 20), and often there was a sudden, pronounced surge of biting activity lasting for only one or two catch periods. An extreme example occurred on April 13 at the Tiroteos site where over one-half of the individuals taken there at ground level were captured during a single catch period. A nightly pattern of vertical movement was not apparent from the biting catches. On many of the nights there appeared to be a synchronization of biting activity at the three vertical levels. An insufficient number of catches was made at the three forest sites to determine between-site differences in the temporal patterns of biting activity. However, the biting activity of *L. yuilli* during the first catch period after sunset tended to be relatively high at the Buenos Aires and Providencia sites but was very reduced at the Tiroteos site.

The summary temporal patterns of the man-biting activity of *L. panamensis* for the forest and clearing habitats were rather similar (Fig. 14). This was also true of the modified geometric means of each catch period (Tables 18 and 19); however, the means for

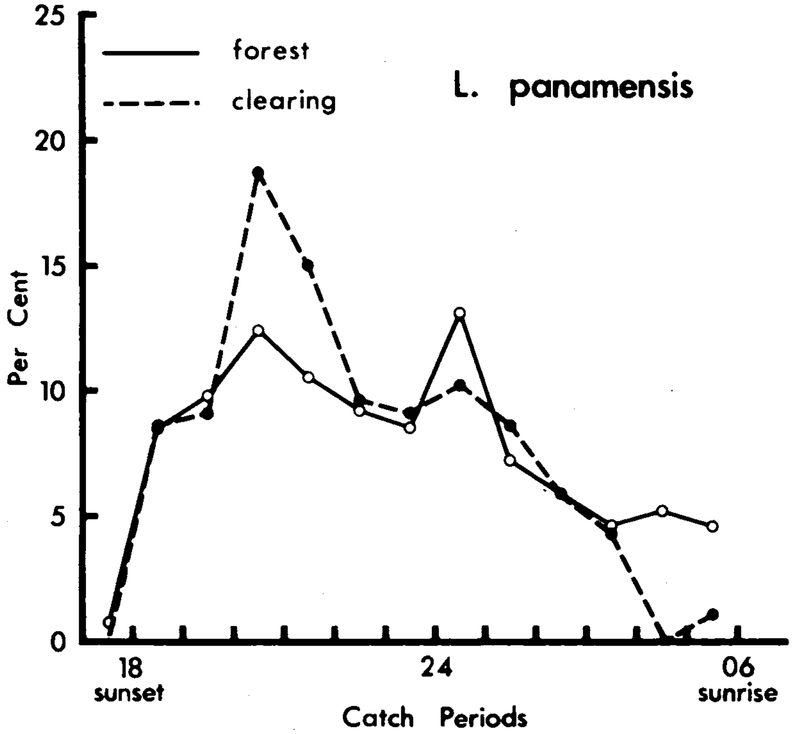

Fig. 14. Summary temporal patterns of man-biting activity in forest and clearing habitats by *L. panamensis* based on modified geometric means converted to percentages. Each catch period approximates the corresponding hour as described in the text.

catch periods 20 and 21 were noticeably greater for the clearing than the forest. Another apparent difference was that only one individual of *L. panamensis* was taken in the clearing during the two catch periods preceding sunrise. Biting activity within the forest tended to be rather sporadic during the night, and there was no apparent evidence of a synchronization of biting activity over the three vertical levels. Thus, Fig. 14 provides only an indication of when biting is most likely to occur during the night.

L. ayrozai was not abundant in the man-biting catches. Its biting activity occurred primarily at ground level and at the Buenos Aires site. Although this species was taken in most of the night catches at the Buenos Aires site, its biting activity was sporadic throughout the night. When summarized over all of the catch nights, the biting activity of *L. ayrozai* was concentrated between about 1900 hours and midnight (Fig. 21).

The man-biting activity of *L. bifoliata* at the forest sites was distinctly concentrated in the first two catch periods after sunset (Fig. 22).

The summary temporal patterns of man-biting activity for *L. gomezi* and *W. rotundipennis* in the clearing are presented in Figs. 23 and 24. There was a distinct peak in the biting activity of *L. gomezi* during the first two catch periods after sunset. A second, smaller peak occurred in the catch period preceding sunrise. In April, a collection was made at each of the six clearing sites for the first catch period after sunrise. A total of 15 phlebotomine sand flies was obtained, 13 of which were *L. gomezi.* Phlebotominae were rarely taken in the series of daytime catches in the clearing, indicating that *L. gomezi* was not active after 0700 hours. The biting activity of *W. rotundipennis* in the clearing occurred primarily before midnight (Fig. 24). *L. gomezi* and *W. rotundipennis* occurred in relatively small numbers in the forest series of catches and the temporal distribution of specimens taken is presented in Table 22. Although the biting activity of *L.*

gomezi tended to be of slightly greater frequency during the first catch period after sunset, there was no distinct concentration of biting activity such as occurred in the clearing.

SEASONALITY OF MAN-BITING ACTIVITY

Since only three, and in some instances two, night forest catches were made per month (see page 94), the seasonal patterns presented in Table 23 are crude. The seasonal pattern of man-biting activity for all of the species combined was relatively uniform and did not decrease appreciably during the December through March dry season, although the rainfall for this period was abnormally high. The seasonal pattern of the biting activity of *L. hartmanni* resembled that of the composite population. The seasonal pattern of *L. trapidoi* was rather erratic but did not have a noticeable decline during the dry season. *L. panamensis* had the most distinctive seasonal pattern with a definite peak occurring in June and July. During the six-month period from March to August in which series of clearing night catches was made, *L. panamensis* was most numerous in the June catches while all of the other common species were most abundant in the March catches.

DISCUSSION

DEFINITION OF TERMS

For clarity, the following terms are defined according to the sense in which they are used in this paper. Assemblage is defined as a group of taxonomically similar populations living within a delimited and relatively uniform geographic area. Hence, the phlebotomine sand fly assemblage includes all of the species of phlebotomine sand flies which occur in the Providencia study area. Community is considered to be more encompassing, i.e., all of the plant and animal assemblages of a given area functioning "as a unit through coupled metabolic transformations" (Odum 1971). The term component is used to identify one or more populations that have a unique trait such as a behavioral characteristic. Thus, the anthropophilic species of the phlebotomine sand fly assemblage are commonly referred to as the anthropophilic component. The adjective anthropophilic is used in its literal sense, i.e., attracted to man, and thus does not imply that man is the preferred host. Species composition refers to the proportional representation of the species for a given catch or group of catches.

COMPARISON OF FAUNAS

The phlebotomine sand fly assemblage of the Providencia study area is closely related to the Panamanian fauna. Thirty-one of the 35 identified species from the Providencia study area occur in Panamá (Christensen, 1972)[1]. The four species which have not been found in Panamá are *L. bifoliata, L. cirrita, L.* sp. near *osornoi*, and *L. yuilli*. Relatively few light trap collections were studied; therefore, the actual number of species occurring in the Providencia study area is probably larger than that given in the appendix.

Since the same collecting methods, i.e., light traps, aspiration from tree trunks, and man-biting catches, were used at a site in Panamá (Chaniotis et al. 1971a and b), at a site in the Department of Chocó, Colombia (Young 1971), and at the Providencia study area, a comparison of the phlebotomine sand fly assemblages seems valid. The Panamá and Chocó sites will be described in two succeeding paragraphs. Thirty-seven species were identified at the Panamá location; 35, at the Curiche, Chocó site; and 35, in the Providencia area. Of the 35 species found in the Providencia area, 22 (63%) occurred in the Panamanian study area and 24 (69%) were found at the Chocó site. The Chocó site had 25 (71%) of its species in common with the Panamanian site. In addition, 17 of the 19 species listed in the Río Raposo study (Department of Valle, Colombia) (Barreto 1969) occurred in the Providencia study

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[1] This includes *L. nocticola* Young which is a recent addiction to the Panamanian fauna (D. G. Young personal communication). Following the advice of D. G. Young (personal communication), *L. tintinnabula* Christensen and Fairchild is considered in this paper as a junior synonym of *L. ayrozai*.

area. The Río Raposo study had 17 species in common with the Chocó site and 15 with the Panamanian.

In spite of the rather high degree of similarity in species composition between the Providencia, Chocó, and Panamanian sites, the anthropophilic components were rather distinct, especially with regard to the predominant species. In the forest series of catches at the Providencia study area, the predominant man-biting species and the percent of the catch attributed to each were *L. hartmanni*, 56%; *L. trapidoi*, 22%; and *L. yuilli*, 13%. Species taken less frequently included *L. panamensis*, 3%; *L. ayrozai*, 1%; *L. bifoliata*, 1%; *L. gomezi*, 1%; and *W. rotundipennis*, 1%.

Apparently, the series of man-biting collections carried out by Young (1971) in the Department of Chocó provide the only other quantitative data on Phlebotominae biting activity in Colombia. His catches were made at four different sites between March and December of 1967. These catches are not strictly comparable with ours since they were made primarily at ground level and only between 1830 and 2100 hours. However, they do indicate that the anthropophilic component in northwestern Chocó was considerably different from that of the Providencia study area in east central Antioquia. The most extensive series of catches (3,763 specimens) was made in a mixed evergreen forest (Tropical Wet Forest Life Zone) at Curiche Camp. The forest was about 0.5 km from the Pacific coast and was at an elevation of between 1 and 12 m. The predominant species and the percentage of the total catch attributed to each were *L. panamensis*, 47%; *L. hartmanni*, 19%; *L. sanguinaria* (Faichild and Hertig), 11% and *L. recurva* Young (reported as sp. "A"), 10%. Species taken less frequently included *L. pessoana* (Barretto), 4%; *L. ayrozai*, 4%; *L. guyanensis* (Floch and Abonnenc) (reported as *L. geniculata* [Mangabeira]), 3% and *L. trapidoi*, 1%. A small series of catches, made at a site (Alto Curiche) about 3.5 km farther inland and at an elevation of 302 m, gave rather similar results although *L. trapidoi* accounted for 7% of the catch and *L. recurva*, only 3%. Another small series of catches was made in a "semi-cleared primary forest" which periodically became flooded. This site was known as Teresita and the area was classified as being within the Transitional Tropical Moist/Wet Forest Life Zone of Holdridge (Eldridge et al. 1973). The forest was about 52 km from the Pacific coast and was at an elevation of 35 m. *L. panamensis* accounted for 87% of the 588 specimens taken at this site; *L. pessoana* accounted for 7% and *L. hartmanni*, 2%. For a more detailed environmental description of Curiche Camp, Alto Curiche, and Teresita, see Eldridge et al. (1973).

The most comprehensive study of the man-biting activity of Phlebotominae in Panamá is that of Chaniotis et al. (1971b). Their study was made in a mature forest characterized as transitional between tropical moist forest and tropical dry forest. The elevation varied from about 50 to 180 m. The area was reported to have a distinct dry season and a mean annual rainfall of 204 cm. Their catches were made both on the ground and in the canopy. The predominant species and the percent of the total catch attributed to each were *L. pessoana*, 40%; *L. trapidoi*, 38%; and *L. panamensis*, 12% Species encountered less frequently included *L. sanguinaria*, 6%; *L. gomezi*, 2%; *L. olmeca bicolor* (reported as *L. olmeca* [Vargas and Diaz-Najera)], 1%; and *L. ylephiletor*, 1%.

The anthropophilic component at the Providencia study area was very distinct from those of more distant regions where studies have been made. With the exception of *L. panamensis* and *L. shannoni*, the man-biting species encountered in Belize by Williams (1966 and 1970a) were different from those of the Providencia area. Although *L. shannoni* was commonly found resting on tree trunks at the Providencia study area, it was rarely taken in the biting catches. *L. olmeca olmeca* (reported as *L. olmeca* [Vargas and Diaz-Najera]), a species which feeds primarily on small terrestrial mammals (Williams 1965, Disney 1968, and Lewis 1975a), was occasionally taken in the man-biting catches in Belize. The closely related *L. olmeca bicolor* accounted for 3.2% of the specimens taken in a series of man-biting col-

Table 15. Specieswise comparisons of abundance patterns across the six clearing sites.[a]

Comparison	F for interaction between species and sites	F for relative abundance	95% confidence interval for abundance ratio[b]	95% confidence intervals for abundance ratio at individual sites[b]					
				A	B	C	D	E	F
L. hartmanni vs *L. gomezi*	12.16**	48.96**		3.95-86.60	3.45-10.14	0.61-1.79	10.73-213.79	1.44-13.25	1.33-5.37
L. hartmanni vs *W. rotundipennis*	3.20*	88.21**		2.03-15.46	2.57-16.08	0.77-4.70	2.10-40.14	5.40-40.83	2.11-6.69
L. hartmanni vs *L. panamensis*	0.21	140.57**	16.38-52.02						
L. hartmanni vs *L. yuilli*	4.75**	151.73**		13.58-121.70	80.48-594.70	5.38-135.46	3.32-76.97	2.54-28.57	2.64-74.95
L. hartmanni vs *L. trapidoi*	2.01	358.83**	29.07-65.26						
L. gomezi vs *W. rotundipennis*	1.19	2.17	0.85-2.69						
L. gomezi vs *L. panamensis*	3.09*	17.91**		0.63-7.64	1.85-21.45	4.70-65.15	0.02-13.51	0.49-55.04	1.88-112.24
L. gomezi vs *L. yuilli*	11.52**	18.16**		0.63-7.64	11.19-122.31	4.85-137.09	0.05-2.43	0.63-6.03	1.27-21.80
L. gomezi vs *L. trapidoi*	7.41**	27.62**		0.16-23.63	7.46-37.13	13.39-245.61	0.08-3.67	0.95-14.26	5.38-140.49
W. rotundipennis vs *L. panamensis*	0.72	5.58*	1.08-2.85						
W. rotundipennis vs *L. yuilli*	4.04**	9.11**		0.26-20.65	2.89-120.95	2.59-63.53	0.13-4.44	0.07-2.83	0.71-14.44
W. rotundipennis vs *L. trapidoi*	2.99*	15.69**		0.09-46.85	1.40-50.76	8.22-98.80	0.11-14.81	0.18-3.79	2.54-110.82
L. panamensis vs *L. yuilli*	1.23	0.02	0.43-2.08						
L. panamensis vs *L. trapidoi*	0.53	1.42	0.75-2.95						
L. yuilli vs *L. trapidoi*	1.45	2.31	0.35-1.16						

[a] The transformation $\log_e(x + 1.0)$ was used for *L. hartmanni* vs *W. rotundipennis* and *W. rotundipennis* vs *L. panamensis*. The transformation $\log_e(x + 0.1)$ was used for all other comparisons. In these transformations x is the total catch of a species for a given night and site. See text for method of transformation selection.

[b] Whenever the F ratio for interaction between sites and the two species was statistically significant, a separate confidence interval was computed for each site. When it was not statistically significant, a single confidence interval was computed. Note that the confidence interval inclues 1.0 (ratio 1:1) whenever the main effect F for difference in abundance is not statistically significant.

* $P \leq 0.05$

** $P \leq 0.01$

Table 16. Diversity and evenness of Phlebotominae man-biting activity at the six clearing sites.

Site	Species diversity[a] H'	Species evenness[a] J'
A	0.86	0.48
B	0.92	0.47
C	1.37	0.70
D	1.28	0.58
E	1.39	0.58
F	1.52	0.69

[a] Natural logarithms ($\log_e$) were employed.

Table 17. Summary by catch period of all individuals, regardless of species, taken in the night catches for the forest and clearing habitats.

	Forest			Clearing		
Catch period	No. of catch periods	No. taken	M_W[a]	No. of catch periods	No. taken	M_W
17	96	8	.1	30	0	.0
18	99	531	2.0	36	220	3.0
19	93	1,159	4.5	36	419	5.7
20	102	1,116	4.5	36	359	4.9
21	96	1,380	5.7	36	343	4.8
22	90	1,064	5.3	36	239	4.0
23	87	953	6.0	36	144	2.4
24	81	893	5.9	36	225	2.5
01	69	791	5.3	36	141	1.7
02	72	723	5.8	36	116	1.5
03	66	655	4.4	36	69	1.2
04	69	506	3.3	36	77	1.1
05	63	250	1.6	36	85	1.3
TOTALS	1,083	10,029	—	462	2,437	—

[a] M_W is a modified geometric mean catch per period. See text for definition.

lections made in eastern Panamá (Christensen et al. 1972) and was rarely encountered biting man in the Providencia area. Studies in the Serra dos Carajás, Pará State, Brazil by Ward et al.(1973) also revealed a very different anthropophilic component. *L. gomezi* and *L. shannoni* were the only man-biting species that the Brazilian and Providencia areas had in common. All of the species taken in ground level man-biting catches in Surinam by Wijers and Linger (1966) were different from those occurring at the Providencia study area.

MAN-BITING ACTIVITY IN THE FORESTS: VERTICAL STRATIFICATION AND BETWEEN-SITE DIFERENCES

The vertical stratification of each species' biting activity tended to be quite variable between the three forest sites and thus a discussion of vertical stratification necessarily includes between-site differences. Differences in biting activity by individual species between the forest sites may be due either to simply a greater amount of biting activity at one site relative to another or to distinct variations in vertical stratification. To varying degrees these differences usually occur together as in the case of the biting activity of *L. hartmanni* at the Tiroteos site relative to the other forest sites. The modified geometric mean catches of *L. hartmanni* at the Buenos Aires and Providencia sites were over twice as large as that at the Tiroteos site (Table 11). In addition, the biting activity of this species at the Tiroteos site was detected to be significantly greater in the understory than in the canopy (Table 5) while at the other sites it was significantly greater in the canopy relative to the understory.

Table 18. Summary by catch period of individuals taken in the forest night catches. The three levels are combined.

Catch period	No. of catch periods	*L. hartmanni* No. taken	*L. hartmanni* M_W[a]	*L. panamensis* No. taken	*L. panamensis* M_W	*L. ayrozai* No. taken	*L. ayrozai* M_W	*L. bifoliata* No. taken	*L. bifoliata* M_W	*L. trapidoi*[b] No. taken	*L. trapidoi*[b] M_W	*L. yuilli*[b] No. taken	*L. yuilli*[b] M_W
17	96	0	0.00	2	0.01	0	0.00	01	0.01	3	0.02	0	0.00
18	99	222	1.05	24	0.13	4	0.03	41	0.20	49	0.24	87	0.44
19	93	719	3.25	38	0.15	17	0.07	19	0.13	119	0.71	134	0.64
20	102	702	2.85	41	0.19	41	0.09	8	0.06	137	0.73	104	0.51
21	96	795	3.88	84	0.16	19	0.10	8	0.05	213	1.16	116	0.63
22	90	658	3.74	31	0.14	25	0.08	5	0.04	190	0.90	76	0.36
23	87	567	3.73	25	0.13	17	0.10	4	0.03	199	1.19	86	0.52
24	81	492	3.70	25	0.20	6	0.05	5	0.04	251	1.42	65	0.39
01	69	328	2.76	13	0.11	4	0.04	0	0.00	220	1.15	197	0.80
02	72	371	2.96	12	0.09	3	0.03	2	0.02	231	1.39	92	0.75
03	66	259	2.14	7	0.07	3	0.03	3	0.03	232	1.13	130	0.72
04	69	206	1.48	12	0.08	2	0.02	1	0.01	206	1.08	66	0.53
05	63	103	0.89	10	0.07	0	0.00	8	0.05	62	0.37	51	0.30
Totals	—	5,422	—	324	—	141	—	105	—	2,112	—	1,204	—

[a] M_W is a modified geometric mean catch per period. See text for definition.

[b] The number of catch periods (collections) was 9 less than that given for catch periods 17-23 and 3 less, for 24,01 and 05. *L. trapidoi* and *L. yuilli* were not distinguished in the first three night catches and thus these catches are not included.

Table 19. Summary by catch period of individuals taken in the clearing night catches for the more abundant species.

		L. hartmanni		*L. trapidoi*		*L. yuilli*		*L. panamensis*		*L. gomezi*		*L. rotundipennis*	
Catch period	No. of catch periods	No. taken	M_W[a]	No. taken	M_W	No. taken	M_W	No. taken	M_W	No. taken	M_W	No. taken	M_W
17	30	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
18	36	61	1.05	8	0.16	28	0.35	9	0.16	96	1.47	9	0.17
19	36	216	3.25	20	0.23	50	0.49	16	0.17	73	0.94	31	0.43
20	36	206	3.17	7	0.13	41	0.35	31	0.35	36	0.57	35	0.48
21	36	206	3.28	12	0.18	32	0.41	27	0.28	24	0.44	41	0.70
22	36	137	2.40	6	0.11	13	0.19	9	0.18	23	0.38	51	0.73
23	36	96	1.66	4	0.08	6	0.10	9	0.17	10	0.15	15	0.28
24	36	128	1.64	6	0.10	37	0.34	11	0.19	29	0.29	11	0.16
01	36	88	1.08	7	0.13	7	0.11	9	0.16	20	0.31	9	0.16
02	36	72	0.89	5	0.09	7	0.10	7	0.11	17	0.27	7	0.13
03	36	56	1.07	0	0.00	4	0.07	4	0.08	3	0.06	2	0.04
04	36	63	0.93	1	0.02	1	0.02	0	0.00	6	0.10	6	0.11
05	36	32	0.46	1	0.02	1	0.02	1	0.02	47	0.69	2	0.04
Totals		1,361	—	77	—	227	—	133	—	384	—	219	—

[a] M_W is a modified geometric mean catch per period. See text for definition.

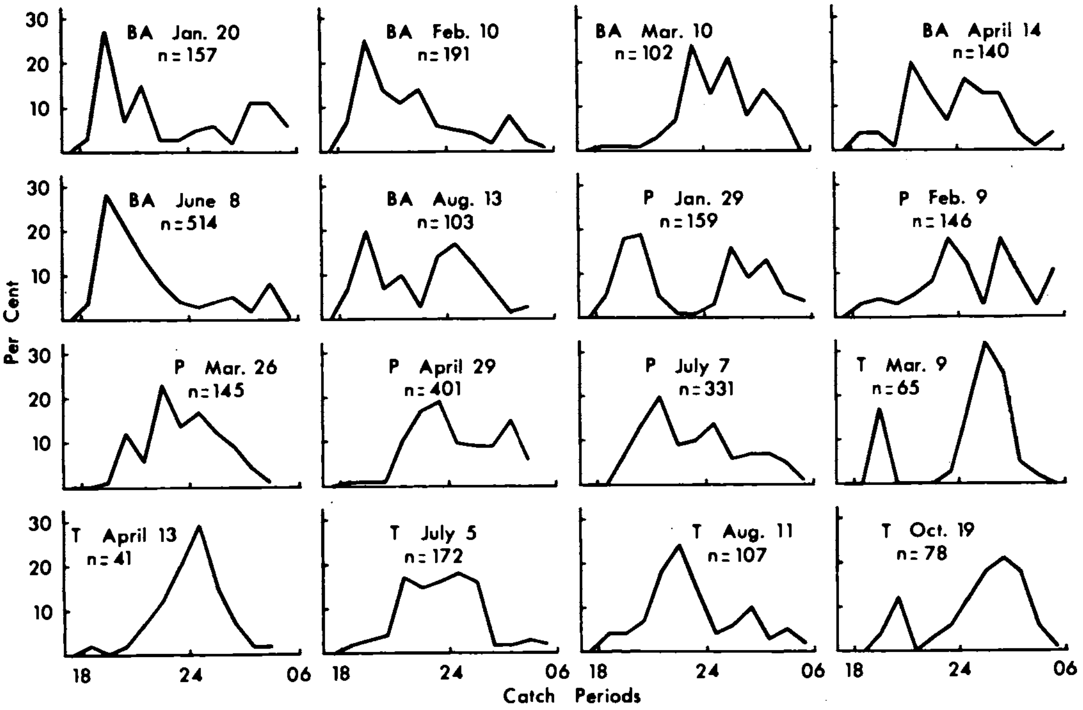

Fig. 15. Variation between nights in the temporal pattern of the man-biting activity of *L. hartmanni* for selected forest catches. Key to symbols: BA = Buenos Aires 1 platform site, P = Providencia platform site, T = Tiroteos platform site, and n = the total number of individuals of this species taken throughout the night for all three vertical levels combined. All dates are for 1971.

The significantly greater amount of biting activity in the canopy relative to each of the other levels for all species and sites combined (Table 4) can be attributed to the distinct preference exhibited by nearly all species for the canopy at the Providencia site (Tables 5 and 6). The biting activity of each of the four most abundant forest species, *L. hartmanni, L. trapidoi, L. yuilli,* and *L. panamensis,* was declared to be significantly greater in the canopy than at ground level (Table 4). This was primarily due to the marked concentration of their biting activity in the canopy at the Providencia site, although *L. trapidoi* was taken in quite low numbers on the forest floor at all three sites. The vertical stratification and between-site variability of biting activity by individual species will be elaborated upon in the discussion of each species.

Other studies of vertical stratification using humans as bait have shown the biting activity of all species combined to be either rather similar between levels (Johnson et al. 1963, Williams 1970a, and Chaniotis et al. 1971b) or distinctly greater at ground level (Ward et al. 1973). In Panamá, Chaniotis et al. (1971b) found the magnitude of biting activity at the ground and canopy levels to be quite similar (ground, 51%; canopy, 49%) for all species combined. Two of the three most abundant species in their study showed a strong preference for the forest floor. The pattern of vertical stratification obtained by Williams (1970a) in an area of "medium bush" in Belize was ground, 29%; understory, 36%; and canopy, 35%. *L. panamensis* was the only species frequently taken in his catches to show a preference for the forest floor. Ward et al. (1973) have described a 4-hour catch they made in Pará State, Brazil in which biting activity was distinctly concentrated at ground level.

Buenos Aires 1 forest site. At the Buenos Aires site, man-biting activity was dominated by the three predominant forest spe-

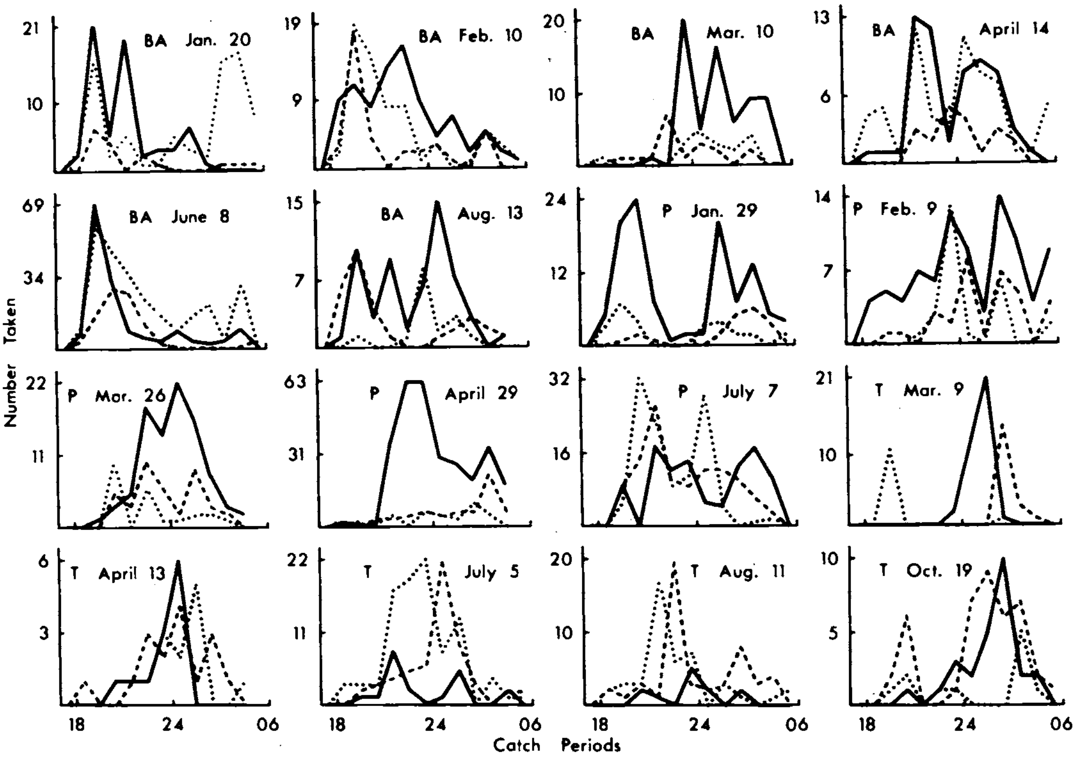

Fig. 16. Nightly temporal patterns of the man-biting activity of *L. hartmanni* partitioned by vertical level. The scales have been adjusted so that the greatest ordinate in each graph is of the same height. Key to symbols: the solid, dashed, and dotted lines represent biting activity at the canopy, understory, and ground levels, respectively; BA = Buenos Aires 1 platform site, P = Providencia platform site, and T = Tiroteos platform site. All dates are for 1971.

cies, i.e., *L. hartmanni, L. trapidoi,* and *L. yuilli.* In addition to these three species, the canopy catches frequently contained *L. panamensis.* The species composition of the understory catches at this site was quite similar to that of the canopy, although the magnitude of biting activity of each species was substantially reduced (Tables 5 and 6). However, at ground level the species composition tended to be somewhat different from that of the canopy and understory. This variation can be primarily attributed to the substantially lower percentage of *L. trapidoi* relative to *L. hartmanni* and the frequent presence of *L. ayrozai.*

The terrain of the Buenos Aires forest was steeply sloped in the vicinity of the platform sites, and as a consequence the canopy was uneven and rather broken. Since the canopy did not provide a continuous closed layer, the microclimatic differences between the canopy and the lower levels were somewhat reduced. There were scattered areas where fairly intense light penetrated to the forest floor. This was evident from the presence of a few herbaceous plants (including species of the Araceae and Marantaceae) in the undergrowth. In this type of an environment the acceptable microclimate of an arboreal species is likely to extend groundward from the canopy. This would appear to account at least in part for the relatively high amount of biting activity that occurred at ground level, especially by *L. hartmanni.* However, one might also expect that the amount of biting activity in the understory by arboreal species such as *L. trapidoi* would be somewhat higher than that for the forest floor (Table 6).

Tiroteos forest site. With regard to species composition, the canopy and understory

Table 20. The temporal distribution of diurnal man-biting activity within the forest for each species taken in the daytime catches[a]

Catch Periods	No. of Catch Period	*L. bifoliata*	*L. gomezi*	*L. hartmanni*	*L. olmeca bicolor*	*L. trapidoi*	*L. yuilli*	*L. panamensis*	*L. ayrozai*
07	156	1	1	2	-[b]	1	4	3	-
08	168	1	-	1	-	2	-	1	-
09	174	-	1	2	1	3	-	1	-
10	174	-	-	2	-	-	1	2	1
11	174	-	2	-	-	2	-	2	-
12	171	-	-	-	-	-	-	-	-
13	171	-	-	-	-	-	1	1	-
14	171	-	-	-	-	4	-	-	-
15	171	-	-	-	-	3	-	2	-
16	150	-	-	-	-	2	-	1	-
TOTALS		2	4	7	1	17	6	13	1

[a] Summarized over sites and vertical levels. The diurnal catch period 17 is included in Table 18 with the nocturnal catch periods.

[b] A dash indicates that no specimens were encountered.

catches at the Tiroteos site were quite similar to the Buenos Aires canopy catches. The most noticeable differences were that at the Tiroteos site the ratio of *L. trapidoi* to *L. hartmanni* approached unity and there was a somewhat greater abundance of *L. bifoliata.* The ground level Tiroteos catches were quite similar in species composition to the forest floor catches at the Buenos Aires site. The most apparent difference was the greater abundance of *L. ayrozai* in the Buenos Aires catches. The magnitudes of biting activity of *L. hartmanni, L. trapidoi,* and *L. yuilli* in the canopy and on the ground at the Tiroteos site were considerably lower than those at the Buenos Aires site (Tables 6 and 10).

Previous disturbance by man was most noticeable in the Tiroteos forest. Some selective cutting in the past, not apparent in the immediate environs of the platform, has resulted in a reduced density of large trees and an incomplete upper canopy in portions of the forest. In addition, the site is located near the top of a south-facing slope. This somewhat drier environment may be less suitable for larval development and adult survival (Johnson and Hertig 1961 and Chaniotis 1975).

With an incomplete upper canopy, environmental differences between the canopy and the understory are likely to be reduced. and as a result differences in both the species composition and magnitude of biting activity between these two levels would also tend to be diminished. This is apparently what has happened at the Tiroteos site (Tables 5 and 6). Haddow (1961a) has observed a similar pattern of vertical distribution by the diurnal, arboreal *Aedes longipalpis* (Grünb.) in an African rain forest with a relatively open canopy. For a number of diurnal, arboreal mosquitoes in Panamá, Trapido and Galindo (1957) have found that the percentage of biting activity occurring in the canopy is greater in rain forest than in tropical deciduous forest. They have also observed that arboreal mosquitoes may be found near the forest floor where the canopy has been broken by a small clearing which may be no bigger than that resulting from the removal of a single large tree. Although some environmental parameters such as relative humidity and light may be the same throughout much of the night at all levels within a rain forest, most individuals are apparently able to orient to a preferred vertical level. Thus, when environmental differences between the canopy and understory are reduced by a more open canopy, nocturnal, arboreal species also tend to have a broader vertical range of biting activity.

Providencia forest site. At the Providencia site, differences in both the magnitudes of biting activity and species composition of the catches were most pronounced between the canopy and the other two levels. As previously noted, the biting activity of *L. hartmanni, L. trapidoi,* and *L. yuilli* was markedly concentrated in the canopy at the Providencia site. In addition to these three species, *L. gomezi, L. panamensis, L. bifoliata,* and *W. rotundipennis* were present in nearly all of the canopy catches. The presence of *L. gomezi* and *W. rotundipennis* is thought to reflect this site's proximity to a clearing. The ground and understory catches at the Providencia site appeared to be quite similar, both in species composition and abundance. The biting activity of *L. trapidoi, L. yuilli, L. bifoliata,* and *L. gomezi* at these two levels was greatly reduced from that occurring in the canopy. *L. panamensis* was also taken with considerably less frequency at the understory and ground levels. In fact, *W. rotundipennis* was the second most numerous species on the forest floor. The frequent occurrence of *W. rotundipennis* and the sporadic presence of *L. yuilli* and *L. ayrozai* distinguished the ground level catches of the Providencia site from those of the other two sites.

Although the Providencia site was located on a steep hillside, the slope in the vicinity of the platforms was gentle. The upper canopy was quite dense, and thus even though this site was situated only about 50 m from a large clearing, the lower levels were well shaded. Since change in a vertical microclimatic gradient is likely to be more abrupt immediately beneath a closed upper canopy than beneath a relatively open one, the environmentally preferred range of a canopy species would tend to be more sharply delimited and vertically compressed in a forest with a dense upper canopy. Thus, an arboreal species would be expected to have a very high percentage of its biting activity in the canopy of such a forest. However, this appears to only partially account for the patterns of vertical stratification at the Providencia site, and other ecological factors related to the site's proximity to a clearing are suspected of also exerting considerable influence.

Summary of forest man-biting activity. The species composition of the forest catches was most dissimilar between the ground and canopy microenvironments. The degree to which the understory catches resembled those for the ground and canopy levels appeared to be at least partially dependent upon forest structure. Thus, when the forest canopy was relatively open (Tirotes site) the understory catches tended to more closely resemble the canopy catches, but when the canopy was unbroken and dense (Providencia site) the understory catches were more similar to those on the forest floor. The canopy catches at all three sites were composed primarily of *L. hartmanni, L. trapidoi,* and *L. yuilli.* Biting activity on the ground and in the understory was dominated by *L. hartmanni.* The only anthropophilic species distinctive to the forest floor was *L. ayrozai;* however, this species was taken in relatively low numbers and was seldom encountered at the Providencia site.

For most species, variations in the magnitude of their man-biting activity from one site to another were greatest at the canopy and ground levels. Biting activity in the canopy by the three predominant forest species was of a greater magnitude at the Buenos Aires and Providencia sites than at the Tiroteos site, while on the forest floor the activity of these species was greater at the Buenos Aires site than at either of the other two locations. Most of these differences were detected to be statistically significant (Table 10). In the understory, between-site variations in the magnitude of the biting activity of *L. hartmanni* and *L. trapidoi* were slight.

As shown in the preceding paragraphs, variations in vertical stratification exhibited by the common species can be related to dif-

Table 21. Summary of individuals taken in the forest night catches by vertical level and catch period for *L. trapidoi*.

		Ground level		Understory		Canopy	
Catch period	No. of catch periods	No. taken	M_W[a]	No. taken	M_W	No. taken	M_W
17	29	2	0.04	1	0.02	0	0.00
18	30	1	0.02	5	0.12	43	0.66
19	28	18	0.32	20	0.43	81	1.68
20	31	12	0.20	43	0.83	82	1.39
21	29	31	0.57	52	0.89	130	2.41
22	27	25	0.51	38	0.69	127	1.70
23	26	25	0.54	36	0.77	138	2.88
24	26	34	0.66	51	0.98	166	3.30
01	22	7	0.21	20	0.63	193	4.02
02	24	14	0.41	56	1.37	161	3.06
03	22	10	0.29	35	0.88	187	2.99
04	23	11	0.32	36	0.89	159	2.63
05	20	9	0.33	3	0.11	50	0.73
TOTALS		199	—	396	—	1,517	—

[a] M_W is a modified geometric mean catch per period. See text for definition.

ferences in forest structure. The microenvironmental preference of a given species may have evolved in relation to the microenvironmental preference of a preferred host or group of hosts and may be cued by microclimatic variation. Microclimatic differences at the various strata beneath the upper canopy are dependent upon forest structure, and the climatic gradient from the canopy to the forest floor may be either continuous or discontinuous (Richards 1952). Microclimatic variations at the same horizontal level may result from differences in the uniformity of a given tree strata (Richards 1952). At night, temperature, saturation deficit, and light become quite similar at all levels within the forest (Haddow et al. 1947, Haddow and Corbet 1961, and Richards 1952) and also above the canopy (Haddow and Corbet 1961) and in adjacent clearings (Haddow 1945). Since many nocturnal Phlebotominae and Culicidae of the humid tropics have distinct microenvironmental preferences with regard to their biting activity, they appear to be able to orient to a preferred microenvironment such as a forest canopy in spite of a uniform nocturnal environment characterized by stable temperature, humidity, and light conditions.

Selection mechanisms for particular microenvironments with regard to nocturnal biting activity are poorly understood. A species' distribution could be related to host preference; however, Tesh et al. (1972) have shown that host selection by at least some rain forest Phlebotominae is strongly influenced by host availability. Nevertheless, microenvironmental preferences are likely to have evolved in relation to the habits of a preferred host or groups of hosts, but the mechanism by which they are able to distinguish microenvironments at night is not clear. Variations in the patterns of vertical distribution exhibited between the three forest sites used in our study suggest that the species may have been responding to differences in forest structure which may have been manifested in an obscure microclimatic variation. A number of other factors may also influence the microenvironmental preferences for biting activity exhibited by a given species and include diurnal resting sites, proximity of carbohydrate source, flight range, physiological state, and heredity. Local variations in the abundance of phlebotomine sand fly populations have been related to edaphic conditions by Chaniotis et al. (1971a).

MAN-BITING ACTIVITY IN THE CLEARING

Very little attention has been given to the biting activity of Neotropical Phlebotominae in clearings adjacent to forest. Al-

Table. 22. Temporal distribution of man-biting activity of species taken infrequently in the forest night catches.

Catch period	No. of catch periods	*W. rotundipennis*	*L. gomezi*	*L. cirrita*	*L.* sp. near *osorni*	*L. serrana*	*L. olmeca bicolor*	*L. shannoni*
17	96	1	–[a]	–	–	–	1	–
18	99	–	13	–	1	3	2	–
19	93	1	6	9	3	1	–	3
20	102	6	5	9	–	1	–	1
21	96	6	12	5	2	–	1	–
22	90	9	7	2	1	–	–	2
23	87	14	9	–	–	1	1	–
24	81	19	9	1	–	1	1	–
01	69	8	9	2	1	–	–	1
02	72	6	2	1	–	–	1	–
03	66	10	8	–	1	–	–	–
04	69	3	7	–	–	–	–	–
05	63	6	8	–	–	–	–	–
TOTALS		89	95	29	9	7	7	7

[a] A dash indicates that no specimens were encountered.

though sand fly biting activity was reduced within the clearing habitat we studied, the reduction tended to be less than that described by Chaniotis and Correa (1974) in Panamá. They found man-biting activity within the center of a small clearing (25 x 30 m) to be only one-fifteenth of that occurring at a site 50 m away in the forest. From light trap catches, these same authors obtained only about one-fifth as many species in the clearing as in mature forest. Recently, Rutledge et al. (1976) sampled with light traps phlebotomine sand fly density along a 200 m transect which began in mature forest, extended through secondary forest, and ended in a cleared area composed of grasses, forbs, and small trees and shrubs. Their capture rates within mature forest were at least 22 times greater than within the clearing. The mean catch within the secondary forest appeared to be about one-half of that of the mature forest.

Our clearing catches were made at six different microenvironments within a rather large clearing (approx. 17.5 hectares) adjacent to the Providencia forest. The catch sites have already been described in some detail, but it is worth emphasizing that the vegetation within the clearing was diverse and included pasture, cultivation, pioneer, and early secondary forest. In general the magnitude of biting activity varied considerably between the sites and the pattern of variation was not the same for all of the species. With respect to species composition, Fig. 7 suggests that the clearing catches were closely interrelated. Variation in species composition between the clearing sites was related to the distance of the sites from the forest edge and to adjacent plant communities.

Total biting activity at the two edge sites, D and E, was greater than that at the sites within the clearing and the difference was declared to be highly significant (Table 14). Site D was located just within the pasture at the margin of mature forest and was only about 40 m away from the Providencia platform site. Site E was situated just within the pasture at the margin of a 10 to 15 m tall early secondary forest which merged about 100 m away with the mature forest. The significantly greater magnitude of biting activity at the two margin sites can be primarily attributed to *L. hartmanni* which exhibited a preference for the margin sites even though it was the most numerous species at all of the clearing sites. The biting activities of *L. trapidoi*, *L. yuilli*, and *L. panamensis* were also concentrated at the two margin sites, but these species were much less abundant at

Table 23. Summary by month of individuals taken in the forest night catches for all species combined and the more abundant species.

Month:	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
No. of catch periods:	99	102	105	102	81	78	102[a]	126[b]	36	48	51	57
All species												
No. taken	836	885	733	1328	832	835	1525	855	481	706	377	629
$M_W{}^c$	3.65	5.06	2.59	5.18	5.68	4.86	6.44	2.55	6.87	5.28	3.57	5.26
L. hartmanni												
No. taken	375	429	322	582	507	620	703	498	353	374	243	416
M_W	2.19	2.48	1.34	2.50	3.61	3.38	3.47	2.08	5.59	2.66	2.10	3.37
L. panamensis												
No. taken	8	10	13	11	22	58	162	15	5	7	3	8
M_W	0.05	0.07	0.07	0.07	0.13	0.35	0.46	0.07	0.08	0.10	0.04	0.09
L. trapidoi												
No. taken	354	232	186	332	161	63	235	70	72	191	58	155
M_W	0.86	1.07	0.64	0.97	1.06	0.50	1.45	0.45	0.89	1.65	0.72	1.34
L. yuilli												
No. taken	59	181	174	315	81	69	69	29	33	110	58	26
M_W	0.28	0.89	0.70	0.99	0.38	0.49	0.34	0.20	0.46	1.04	0.61	0.28

[a] The number of catch periods for *L. trapidoi* and *L. yuilli* is 84

[b] The number of catch periods for *L. trapidoi* and *L. yuilli* is 81.

[c] M_W is a modified geometric mean catch per period. See text for definition.

these sites than *L. hartmanni.* The biting activity of each of the three prominent forest species, i.e., *L. hartmanni, L. trapidoi,* and *L. yuilli,* was somewhat greater at site E than at site D. These differences can be primarily attributed to a single large catch of all three species at site E in March. The biting activity of *L. gomezi* was also greater at site E than at site D but the difference was declared to be highly significant (Table 14). This disparity is thought to be a reflection of the relatively sheltered nature of site D. Thus, the environment of this site appeared to be rather similar to that of the forest floor, a location where *L. gomezi* was seldom encountered. *W. rotundipennis,* which did not exhibit a distinct vertical preference at the Providencia site, and *L. panamensis* were taken in larger numbers at site D than at site E.

At clearing site F the modified geometric mean catches of *L. hartmanni, L. trapidoi,* and *L. yuilli* were of intermediate magnitude, i.e., they were less than those at the two edge sites but greater than those at sites C, B, and A where, with the exception of *L. hartmanni* at site B, their biting activity was sharply reduced. *L. gomezi* and *W. rotundipennis* were, respectively, the second and third most abundant species at site F, and each had comparatively high magnitudes of biting activity at this site. Clearing site F was situated just within the pasture adjacent to a strip of pioneer vegetation that extended from the mature forest about 130 m away.

Total biting activity at clearing site C was considerably reduced and was detected to be significantly less than at site E, 40 m away (Table 14). Clearing site C was located centrally within the pasture between sites E and F and 30 to 40 m away from other vegetative formations. Most of the biting activity at site C was by *L. hartmanni* and *L. gomezi.* However, on a comparative basis the activity of *L. hartmanni* at this site was found to be significantly less than that at sites E and D (Table 14), and the modified geometric mean catch was only about half as large as that for sites F and B (Table 13). There thus appears to be a genuine reluctance on the part of *L. hartmanni* to enter cleared areas, although it may be quite common in early successional stages adjoining mature forest. *L. gomezi* had a relatively high magnitude of biting activity at site C and almost exceeded *L. hartmanni* in terms of actual numbers taken. *W. rotundipennis* accounted for most of the remaining biting activity at this site (Table 13). The greater biting activity of *L. hartmanni, L. trapidoi,* and *L. yuilli* at site F compared with site C suggests that these species extended well into the clearing along a narrow strip of pioneer vegetation extending from the forest, albeit at relatively low magnitudes, but were very reluctant to enter the pasture.

Total biting activity at clearing site B was slightly greater than at site C but was strongly dominated by *L. hartmanni.* This site was situated within a small grove of fruit trees in an area of diverse cultivation and was approximately 240 m away from mature forest. The modified geometric mean catch of *L. hartmanni* was about twice as large for this site as for site C (Table 13). The catches for site B form a rather distinctive cluster in Fig. 7 indicating they have a rather unique species composition. This can be attributed to the strong dominance of *L. hartmanni,* relatively little biting activity by *L. gomezi* and *W. rotundipennis,* and a virtual absence of *L. trapidoi, L. yuilli,* and *L. panamensis.*

Man-biting activity by phlebotomine sand flies at clearing site A was considerably lower than that at any of the other clearing sites (Table 12) and was strongly dominated by *L. hartmanni.* This site was located at the edge of an early secondary woods and was adjacent to the Río Anorí. Site A was approximately 360 m from the forest adjacent to site D; the closest mature forest was about 280 m to the southwest. The Scheffé pairwise comparisons for all species combined detected statistically significant differences between the magnitude of biting activity occurring at site A and that at sites D, E, and F (Table 14). Although *L. hartmanni* accounted for 77% of the specimens taken at site A, the modified geometric mean catch of this species was quite small, being comparable only to that for site C. The irregular and meager occurrence of other species has resulted in a rather widespread distribution of the catches for site A over the left half of Fig. 7.

Phlebotominae biting activity within a clearing, such as is established for subsistence farming, appears to be dependent upon the subsequent use of the land and whether there is additional clearing of the adjacent forest. Clearing site C can be considered representative of a cleared area that is not allowed to proceed to a secondary successional stage and thus can also be considered as a recent clearing. At this site there was a pronounced reduction in biting activity by the predominant forest species. The failure of *L. hartmanni* to dominate biting activity at this site coupled with substantial activity by *L. gomezi* and *W. rotundipennis* resulted in this site having a comparatively high evenness value for biting activity. If a portion of the clearing is neglected and pioneer vegetation becomes established, the anthropophilic component may become similar to that observed for site F. Although total man-biting activity was somewhat reduced compared with that at the forest edge, diversity of biting activity was greatest at this site. The estimate of the evenness of biting activity was also relatively large for this site. This was the result of a relatively moderate magnitude of biting activity by the forest species and comparatively high magnitudes of activity by the clearing species, i.e., *L. gomezi* and *W. rotundipennis.* The somewhat reduced diversity at site D at the edge of the mature forest is at least partially due to the dominance of *L. hartmanni.*

There is some indication from our studies that those forest species which show a strong vertical microhabitat preference with regard to biting activity, e.g., *L. trapidoi* and *L. ayrozai,* are less tolerant of any of the clearing microenvironments than those species with somewhat weaker preferences, such as *L. hartmanni.* The low values for diversity and evenness at sites A and B are a result of the strong dominance of *L. hartmanni* at these sites which in turn can be at least partially attributed to reductions in biting activity by the other species, especially at site A. This is thought to be more a reflection of the distance of these sites from mature forest than of the particular type of vegetation surrounding the sites.

VARIATIONS IN THE SPECIES COMPOSITION OF THE ANTHROPOPHILIC COMPONENT BETWEEN DIFFERENT MICROENVIRONMENTS

The polar ordination and informal comparisons, such as of the modified geometric means, reveal a number of interesting differences between the forest and clearing catches. Statistical comparisons were not made because of insufficient uniformity between these two series of catches. Comparisons between the forest and clearing should generally be considered with some reservation, especially since the clearing catches were made only over a 6-month period and only at one level. The 6-month interval over which the clearing catches were made extended from March to August and thus included one month of the indistinct dry season.

A total of nine microenvironments were sampled in the night series of forest catches, i.e., the ground, understory, and canopy levels at each of three sites, and six additional ground level microenvironments were sampled in the clearing series of catches. The polar ordination compared and ordinated individual catches made in the above 15 microenvironments on the basis of the occurrence and relative abundance of the eight most frequently encountered species. Variations in species composition between the microenvironments were then expressed graphically. The resulting patterns in Figs. 7 and 8, derived from the first three ordination axes, suggest certain relationships between species composition and microenvironment which may be related to specific types of vegetation. These figures are somewhat skewed in favor of species presence rather than abundance since a square root transformation was applied to all of the values. This, of course, has tended to minimize the difference between catches with large and small values for the same species and was done to reduce the dominating influence of *L. hartmanni* on the analysis.

Fig. 7 of the first two ordination axes shows the catches for the forest and clearing sites to be quite distinctly separated from each other. This indicates, on the basis of species composition, that the microenvironments sampled at all three forest sites tended to exhibit a greater degree of similarity to each other than to the clearing microenvironments, and conversely the clearing microenvironments tended to be more closely related to each other than to the forest microenvironments.

The largest intercatch distances in Fig. 7 appear to be between the canopy and understory catches at the Buenos Aires and Tiroteos sites on the one hand and clearing site C, the most exposed site, on the other. The catches at these forest microenvironments were quite similar, being composed primarily of *L. hartmanni, L. trapidoi,* and *L. yuilli.* The biting activity at clearing site C was dominated by *L. hartmanni* and *L. gomezi* and to a lesser degree by *W. rotundipennis.* The first axis of the ordination has essentially separated the forest catches from those of the clearing on the basis of the combined biting activities of *L. trapidoi* and *L. yuilli* relative to *L. hartmanni.* This has had the effect of placing most of the catches for the two edge sites, D and E, near the center of the first axis with many of the ground level forest catches which tend to have reduced amounts of *L. trapidoi* and *L. yuilli.* Thus, in Fig. 7 the catches for clearing site D tend to be situated between those for the Providencia and Tiroteos ground level and the Providencia understory microenvironments and those for clearing sites E and F. Many of the clearing site catches have been separated from the ground level forest catches by the second axis which reflects a general reduction in the dominance of *L. hartmanni* in the biting catches from the forest floor to clearing sites, C, F, and E.

The species composition of the canopy catches tended to be quite dissimilar from that of either the ground level or clearing catches. An important difference was in the ratio of *L. hartmanni* to *L. trapidoi* and *L. yuilli* combined. This ratio was closer to unity for the canopy catches than for those of the forest floor and clearing sites where the ratios tended to be decidedly in favor of *L. hartmanni.* The biting activity of *L. trapidoi* was primarily restricted to the forest canopy. This species was very reluctant to enter the clearing. In the clearing catches

L. trapidoi was taken most often at the two edge sites, and the modified geometric mean catches of *L. trapidoi* for these sites were comparable only to that of the very reduced ground level mean catch for the nearby Providencia forest site. The biting activity of *L. yuilli* also tended to be concentrated in the canopy. However, this species was frequently taken at ground level in the relatively open Tiroteos forest and at the edge of the early secondary forest, but like *L. trapidoi,* it was seldom taken at the sites within the clearing.

L. gomezi and *W. rotundipennis* were distinctive to the clearing habitat and the nearby Providencia forest site. Within this forest the biting activity of *L. gomezi* was concentrated in the canopy. This species was taken infrequently in the understory and on the forest floor and also occurred in relatively low numbers at the margin of the forest 40 m away (site D). The variation in biting activity across the clearing sites indicates that *L. gomezi* favored the early secondary forest but also readily entered the pasture. The low magnitude of biting activity by *L. gomezi* at site A, which was about 300 m from mature forest, suggests that while this species readily enters clearings, it is reluctant to extend more than a few hundred meters into them. The patterns of man-biting activity exhibited by *L. gomezi,* including its distinctly crepuscular diel pattern, suggest that this species may be more likely to come in contact with man than any of the other species and should be considered as a potential vector of human disease, at least at the Providencia study area. Although not as abundant as *L. gomezi, W. rotundipennis* was quite common in the clearing catches and appeared to be rather uniformly distributed over much of the clearing. This speices was also frequently taken at the Providencia forest site where it maintained a rather uniform intensity of biting activity over all three vertical levels but was rarely encountered at the other two forest sites. The modified geometric mean catch of *W. rotundipennis* for each of the clearing sites, except for A, exceeded that for each of the three vertical levels of the Providencia platform site by as much as 2.5 times.

A comparison of the modified geometric mean catches of *L. panamensis* for the clearing and forest sites (Tables 11 and 13) indicates that this species had relatively uniform magnitudes of biting activity in both habitats but was most numerous at the ecotonal microenvironments. In Venezuela, Pifano et al. (1960) have observed *L. panamensis* to be abundant at the forest perimeter, especially in areas where trees are being cut. Rutledge et al. (1976) found *L. panamensis* to be virtually absent from light trap catches made within a clearing but to be quite common in catches from adjacent secondary and mature forest.

While making comparisons of biting activity between various forest and clearing sites, we have assumed that the catches obtained at these locations were typical of the microenvironment in which they were made. However, this may not always have been the case as we did not have sufficient resources to implement the night catches at more than one location in the three forests and in the six clearing microenvironments sampled. Highly localized variations in population density and biting activity have been observed for phlebotomine sand flies (Chaniotis et al. 1971a, Lewis 1971, and Shaw and Lainson 1968) and similar variations have also been noted for mosquitoes by Galindo et al. (1950).

DIEL PERIODICITY OF MAN-BITING ACTIVITY

Diurnal biting activity. There was very little diurnal man-biting activity by the Phlebotominae in the Providencia study area. The biting activity of phlebotomine sand flies tends to be primarily crepuscular and nocturnal (Lewis 1971 and Chaniotis et al. 1971b), but diurnal biting near the forest floor has been reported from several regions (Williams 1966 and 1970b, Disney 1968, Chaniotis et al. 1971b, and Ward et al. 1973). In each of these studies by others the daytime activity was dominated by a single species whose biting activity tended to be greater at night and occurred primarily at ground level. Thus, the absence of an avid man-biting species with a distinct preference for the forest floor appears to account for the paucity of diurnal Phlebotominae man-biting activity within the forests of the Providencia study area. *L. ayrozai* was the only species taken in the man-biting catches that exhibited a distinct preference for the forest floor but it was encountered rather infrequently. Table 8 indicates that the meager diurnal biting activity in our study area occurred primarily at the ground and understory levels.

Reliability of summary temporal patterns in representing biting activity. A summarizing pattern of temporal biting activity such as Fig. 11 for *L. hartmanni* represents the mean pattern of many catch nights and can be quite misleading. Haddow and Ssenkubuge (1973) have shown for the primarily nocturnal *Anopheles gambiae* Giles that its rather broad and ill-defined summary pattern of temporal biting activity obscured the fact that there was considerable night to night variation in the temporal pattern and concluded that "considerable caution must be used in this type of analysis, except in well synchronized biting patterns." A comparison of the nightly temporal patterns of biting activity for *L. hartmanni, L. trapidoi,* and *L. yuilli* revealed that each of these species also had a pronounced variation in its biting activity from one night to another. The summarizing patterns of these species are thus representative of biting activity only to the extent that they show the period of time in which biting activity is likely to be concentrated. However, biting cycles characterized by one or two consistent, narrow intervals of biting activity, such as occurs with crepuscular species, tend to be accurately represented by summary patterns. The biting activity of *L. gomezi* in the clearing (Fig. 23) and of L. *bifoliata* in the forest (Fig. 22) appears to be of this type.

The large variability from one night to another in temporal patterns of biting activity in the relatively stable nocturnal environment of a tropical wet forest is difficult to understand. Williams (1966) has suggested that the bimodal biting rhythms he detected for *L. panamensis* and *L. shannoni* may have been related to differences in the biting activity of nulliparous and parous individuals. Haddow and Ssenkubuge (1973) have discussed nocturnal biting cycles of mosquitoes, particularly in relation to the concept developed by Lumsden (1952) in which temporal variations in biting activity may be related to different age groups of the population. They noted, however, that there was considerable evidence in the literature against this concept. Our superficial temperature measurements did not reveal any obvious relation between temperature and biting activity. Haddow and Ssenkubuge (1973) were unable to relate nightly variations in the biting cycle of the nocturnal *Anopheles gambiae* to relatively mild fluctuations in weather although the activity of this species was depressed by heavy rain and wind. The cues, environmental and/or physiological, that control the initiation and ascent components of a nocturnal biting cycle in the rain forest environment are largely unknown. Pifano et al. (1960) have observed that phlebotomine sand flies disperse when the ambient temperature and humidity approach that of their diurnal resting sites. Scorza et al. (1968a) appear to hold a similar opinion. This dispersal may not be directly related to biting activity since there are several circadian activities dependent upon flight.

Colless (1957) has related the rate at which *Culex annulus* arrived at a bait through the night to an equation for a constant rate of depletion. Such a relation is thought to be limited to a rather unique situation in which a number of assumptions have been satisfied. In addition to the two assumptions mentioned by Colless, i.e., random arrival at a host and a "'closed domain'... delimited by geographic features," the equation would also appear to be dependent upon the maintenance of a constant level of biting excitation and relatively stable cimatic condictions. In most situations one or more of these assumptions is not likely to be met. In many areas a given mosquito or sand fly population may extend continuously for a considerable distance. However, most species do have a tendency to aggregate in favorable microenvironments and the rate of dispersion from these foci would be dependent upon the species. Figs. 15, 17, and 18 show that *L. hartmanni,L.*

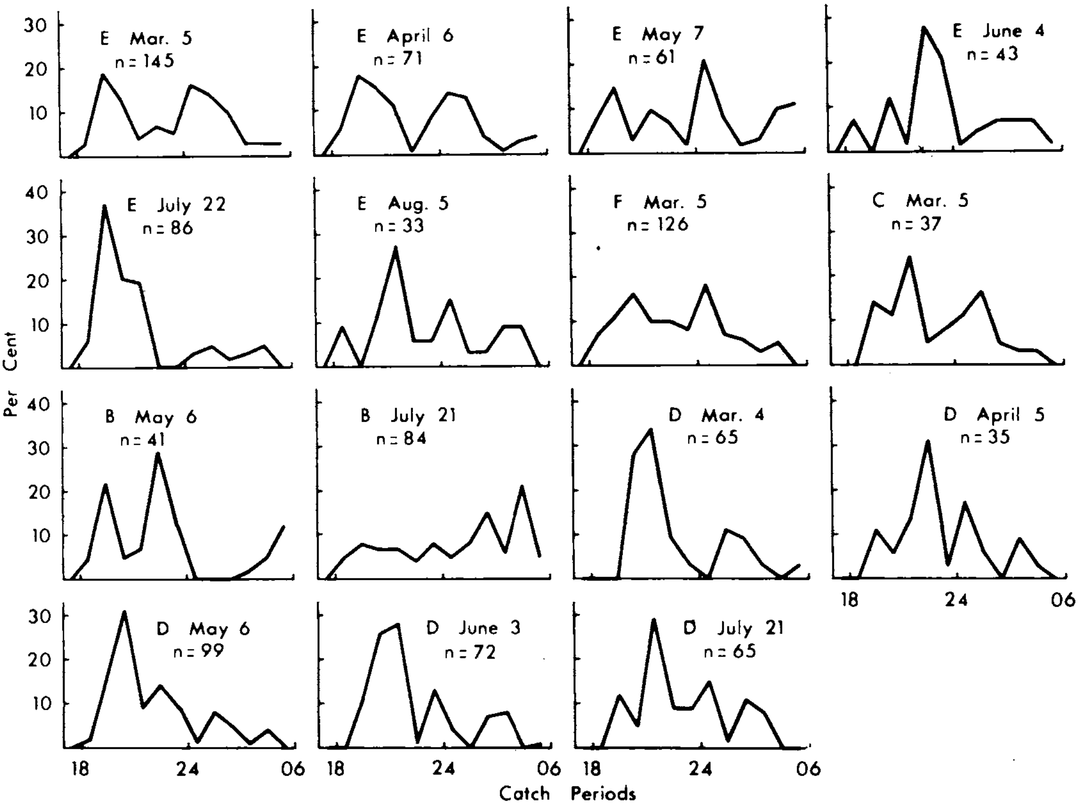

Fig. 17. Variation between nights in the temporal pattern of the man-biting activity of *L. hartmanni* for selected clearing catches. Key to symbols: A to F = the six clearing sites and n = the total number of individuals of this species taken throughout the night. All dates are for 1971.

trapidoi, and *L. yuilli* frequently had prominent but irregular peaks in their nocturnal biting activity which would suggest that the intensity of their biting excitation may fluctuate during the night.

Reduction in biting activity as a component of a biting cycle is likely to result from both the removal of individuals in the proximity of the host stream, i.e., an area of host-conditioned air (Gillies 1972), and a reduction in biting excitation. Sharp declines in biting activity occurred on many nights, particularly in relation to prominent peaks in biting activity. Such rapid reductions are thought to be at least partially due to the depletion of individuals from the vicinity of the host stream, especially in view of the apparently limited flight range and localized distribution of phlebotomine sand flies (Chaniotis et al. 1974). Increases in biting activity also were frequently quite rapid, suggesting that biting excitation was often sudden. As mentioned above, the ascent component of the biting cycles of *L. hartmanni*, *L. trapidoi*, and *L. yuilli* was quite variable with respect to time from one night to another.

There was no indication of a consistent nightly vertical movement by *L. hartmanni*, *L. trapidoi*, or *L. yuilli*. Neither the temporal patterns summarizing biting activity by vertical level (only the patterns for *L. trapidoi* are presented [Fig. 19]) nor a night by night comparison of temporal patterns differentiated by level (Fig. 16) gave an indication of such movement. Haddow (1961a and b) has shown that the crepuscular mosquitoes *Aedes ingrami* Edwards and *Mansonia fuscopennata* (Theobald) make daily vertical migrations from the forest floor to the

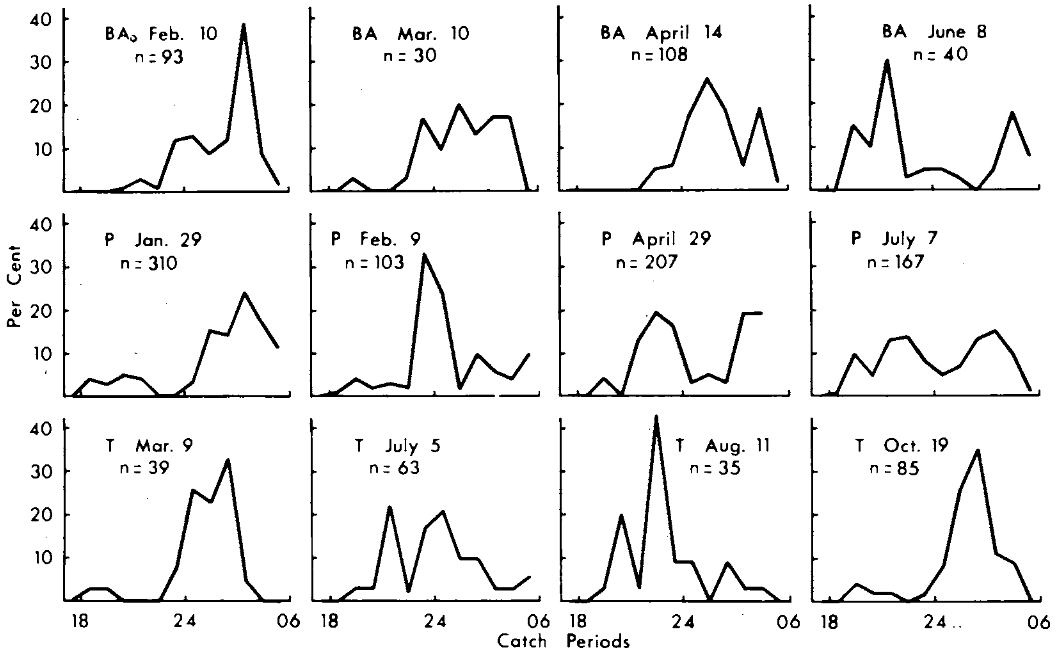

Fig. 18. Variation between nights in the temporal pattern of the man-biting activity of *L. trapidoi* for selected forest catches. Key to symbols: BA = Buenos Aires 1 platform site, P = Providencia platform site, T = Tiroteos platform site, and n = the total number of individuals of this species taken throughout the night for all three vertical levels combined. All dates are for 1971.

canopy. Chaniotis et al. (1974) indicate that *L. trapidoi* moves upward at dusk into the canopy from its diurnal resting sites of which the forest leaf litter may be the preferred (Chaniotis et al. 1972). This pattern of movement was not apparent in our biting studies. On many nights the biting activity of *L. trapidoi* was very low during the first few hours after sunset suggesting that this species may move into the canopy before reaching a high degree of biting excitation. The limited diurnal biting activity of this species was concentrated in the understory. This would suggest that *L. trapidoi* may also rest in the understory and perhaps shaded areas near the canopy. An investigation of the diurnal resting sites of *L. hartmanni* and *L. yulli* has not been made.

A comparison of the summary temporal patterns of biting activity for the forest and clearing catches indicates biting activity tended to occur earlier at the clearing sites than at the forest locations. This was true for *L. hartmanni, L. trapidoi,* and *L. yuilli* although the forest and clearing patterns were quite similar for *L. panamensis* (Figs. 11, 12, 13, and 14). At the clearing sites variability in the temporal pattern of biting activity between individual nights appears to be somewhat dependent upon the site, as the temporal pattern of *L. hartmanni* at site E was considerably more variable than at site D, adjacent to the mature forest (Fig. 17). The modified geometric mean catch of all species combined for the first catch period after sunset was 1.5 times greater for the clearing sites than for the forest sites (Table 17). There was, however, considerable variability in biting activity at this time between the individual clearing sites. The greater magnitude of biting activity in the clearing during the first hour after sunset can be largely attributed to the crepuscular *L. gomezi*. Within the forest only the relatively infrequent *L. bifoliata* exhibited a distinct crepuscular biting cycle. The tendency for biting activity to be con-

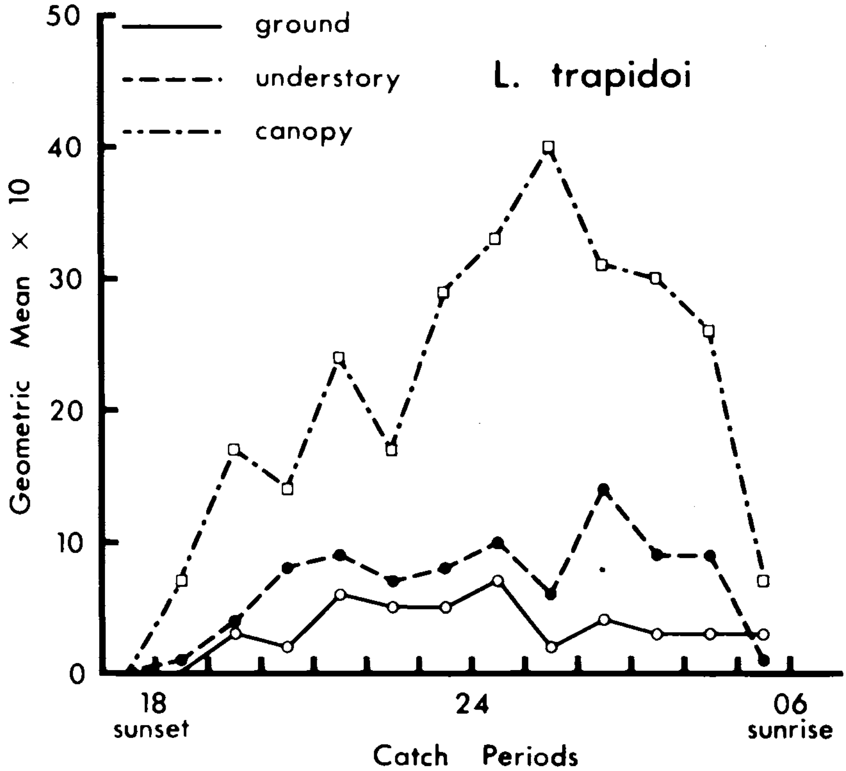

Fig. 19. Summary temporal patterns of man-biting activity at three levels within the forest for *L. trapidoi* based on modified geometric means. Each catch period approximates the corresponding hour as described in the text.

centrated earlier at the clearing sites than within the forest is difficult to rationalize, especially without precise climatic data. Furthermore, we do not know to what extent biting activity within the clearing is due to individuals that moved into the clearing on previous nights and found suitable diurnal resting sites and/or to what extent it is due to flight during the same night from the adjacent forest.

SEASONAL VARIATIONS IN MAN-BITING ACTIVITY

Seasonal fluctuations by the composite population were relatively mild and in general the same was also true for *L. hartmanni.* However, the seasonal patterns of man-biting activity presented in Table 23 must be considered as rough approximations due to small sample size. *L. panamensis* exhibited the most pronounced seasonal fluctuation in man-biting activity, attaining a marked peak in June and July. Seasonal fluctuations in population density characterized by increases during the wet season and decreases in the dry season have been observed for many species (Fairchild and Hertig 1951, Biagi and Biagi 1953, Johnson et al. 1963, Ortiz and Scorza 1963, Scorza et al. 1963, Disney 1968, Scorza et al. 1968b, Lewis 1971, Chaniotis et al. 1971a, and Christensen et al. 1972). A few species such as *L. carpenteri* (Fairchild and Hertig), *L. cruciata* (Coquillet), and *L. permira* (Fairchild and Hertig) appear to be more abundant during the dry season (Chaniotis et al. 1971a, Christensen et al. 1972, and Disney 1968).

The seasonal patterns in Table 23 are also perhaps somewhat atypical from the standpoint that there was an unusually large amount of rain during the 1971 dry season. Chaniotis et al. (1971a) have shown that total sand fly density in the dry season may be

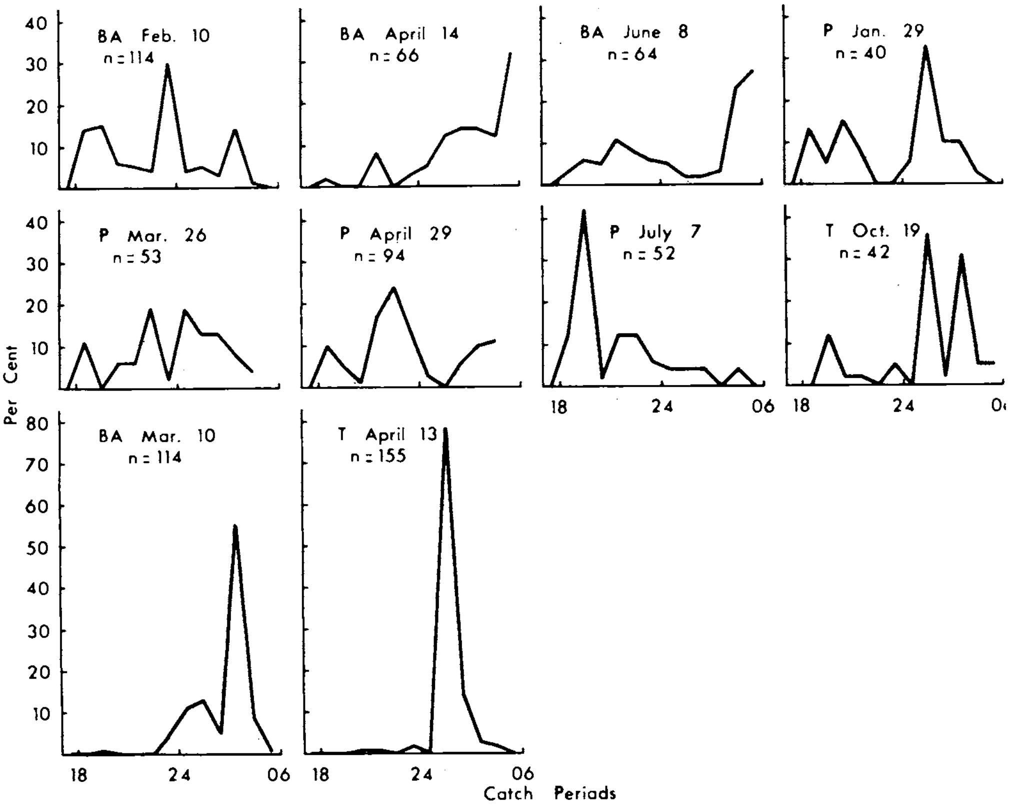

Fig. 20. Variation between nights in the temporal pattern of the man-biting activity of *L. yuilli* for selected forest catches. Key to symbols: BA = Buenos Aires 1 platform site, P = Providencia platform site, T = Tiroteos platform site, and n = the total number of individuals to this species taken throughout the night for all three vertical levels combined. All dates are for 1971.

dependent upon the severity of this season. Thus, during an unusually mild dry season, they obtained considerably larger numbers of most species than they did during the previous dry season when the monthly totals of rainfall were substantially lower and resembled the 10-year mean. However, Chaniotis et al. (1971b) also found that the seasonal patterns of man-biting activity of the three predominant anthropophilic species in their study showed no clear relationship with estimates of population density obtained by other means in the same area over the same time. Accordingly, the seasonal patterns of man-biting activity in Table 23 may not necessarily be accurate representations of population density.

DERIVATION OF INTERSPECIFIC DIFFERENCES IN BITING ACTIVITY

The behavioral differences in biting activity observed between the various species in this study may have evolved more as a result of adaptive specialization than of competition. Downes (1971) considers the Phlebotominae to be one of the most archaic groups of modern Diptera. He suggests that forms similar to those currently in existence were present in the Triassic period, a time when reptiles were dominant and early mammals had not yet begun to develop. Phlebotominae-like species were thus in a position to evolve with the contemporay vertebrates and adapt to their habits. (Paleontological evidence is inconclusive since the oldest known fossils of the subfamily Phlebotominae are from the Lower Cretaceous period [Hennig 1972]. However, these fossils appear to be morphologically quite similar to the modern species.) This coevolution is apparent in present species, some of which appear to be quite host specific and have morphological (Lewis 1975b) and behavioral adaptations which presumably enhance their success in obtaining a blood meal from a preferred host.

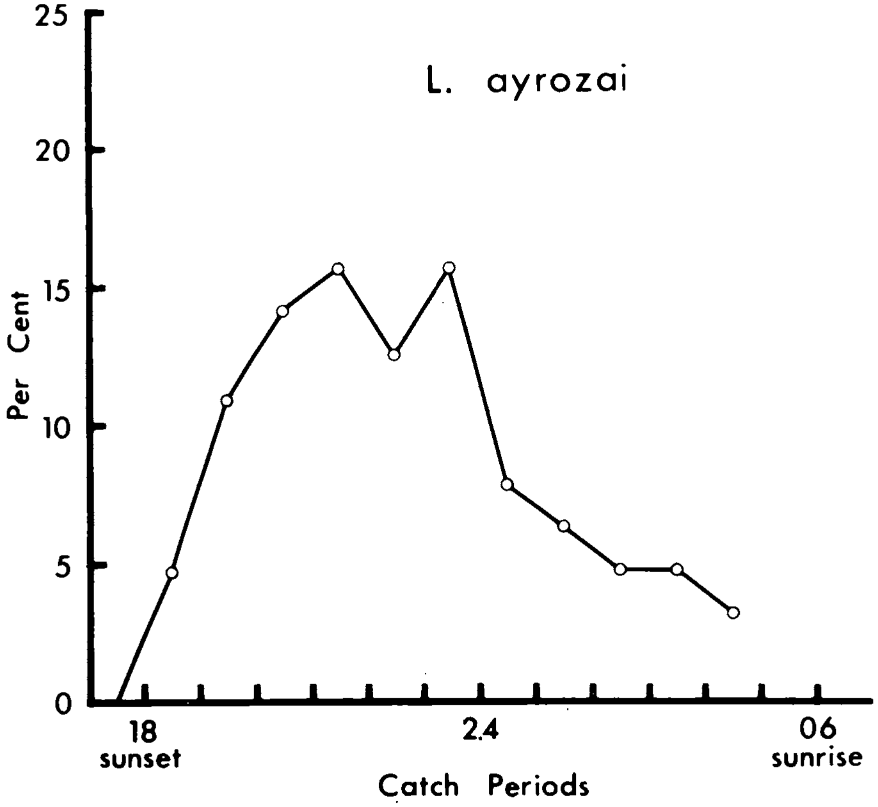

Fig. 21. Summary temporal pattern of man-biting activity in the forest by *L. ayrozai* based on modified geometric means converted to percentages. Each catch period approximates the corresponding hour as described in the text.

The biting activity of others tends to be related to host availability, e.g., those utilizing a broad range of mammals (Tesh et al. 1972). However, even these species, e.g., *L. trapidoi,* may have distinct behavioral patterns related to biting activity. Differences between species which are related to biting activity are thus thought to have evolved primarily from sand fly-host interactions rather than from interspecific competition between sand fly species.

The segment of the phlebotomine sand fly life cycle in which interspecific competition would most likely occur is not readily apparent. Competitive relations with other species could occur with respect to developmental sites, larval food, diurnal resting sites, carbohydrate sources, and blood meals. The larvae of many species develop on the forest floor, and at least some species have a preferred spatial niche such as the soil around certain trees (Rutledge and Ellenwood 1975a, c). While there would likely be an abundance of suitable spatial niches for larval development in a favorable environment, there may be few in a marginal one. Competition could therefore develop in marginal environments between two species utilizing rather similar spatial niches. The larvae of many forest species feed on mold and decomposing organic matter such as dead insects and leaf litter (Johnson and Hertig 1961). Competition for food among larvae is thus likely to be inconsequential. Many species appear to have quite specific microhabitat preferences with regard to their diurnal resting sites, although a preferred microhabitat may be shared with other species (Chaniotis et al. 1972). For most species availability of diurnal resting sites is not likely to be a significant source of interspecific competition since many of the sites used, i.e., tree

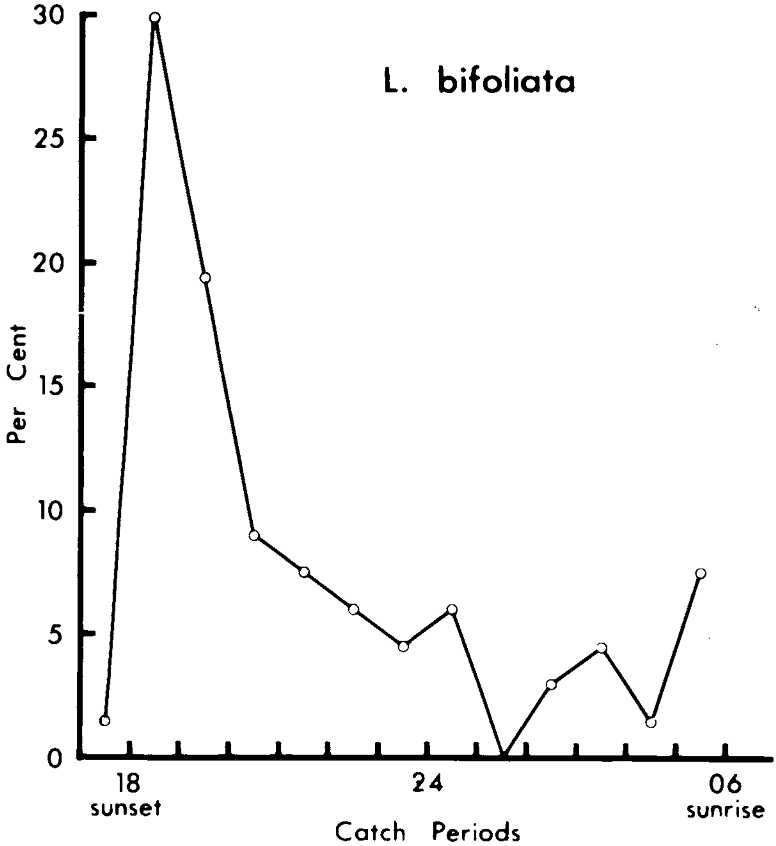

Fig. 22. Summary temporal pattern of man-biting-activity in the forest by *L. bifoliata* based on modified geometric means converted to percentages. Each catch period approximates the corresponding hour as described in the text.

trunks, plants near the forest floor, and leaf litter, would seem to be readily available. However, these resting sites are not homogeneous and only certain portions of them may provide an acceptable microenvironment.

Competition for resting sites would seem most likely to occur in quite disturbed or small isolated forests where specific microhabitats may be very limited. Very little information exists about the sugar feeding habits of adult sand flies in the Neotropical forest environment. Thus, the likelihood of competition for a carbohydrate source cannot be determined. Probable sources of sugar meals include nectar, honey dew, ripe fruit, and plant fluids which become accessible from damaged plant tissue. Competition for the blood of a vertebrate host utilized by two or more species would likely be minimal since the amount of blood taken, even by many individuals, would be insignificant compared to the total volume of blood pressent in a host. Likewise, competition for space on most hosts would be minimal. Some partitioning of the host with respect to the location of biting activity may occur (Lewis 1971).

THE COMMON MAN-BITING SPECIES OF THE PROVIDENCIA STUDY AREA

L. ayrozai (Barretto and Coutinho), 1940

L. ayrozai was described by Barretto and Coutinho (1940) from specimens taken in the State of São Paulo, Brazil. Abonnenc (1948) noted the presence of this species in French Guiana, and Barreto (1969) was the first to report its occurrence in Colombia

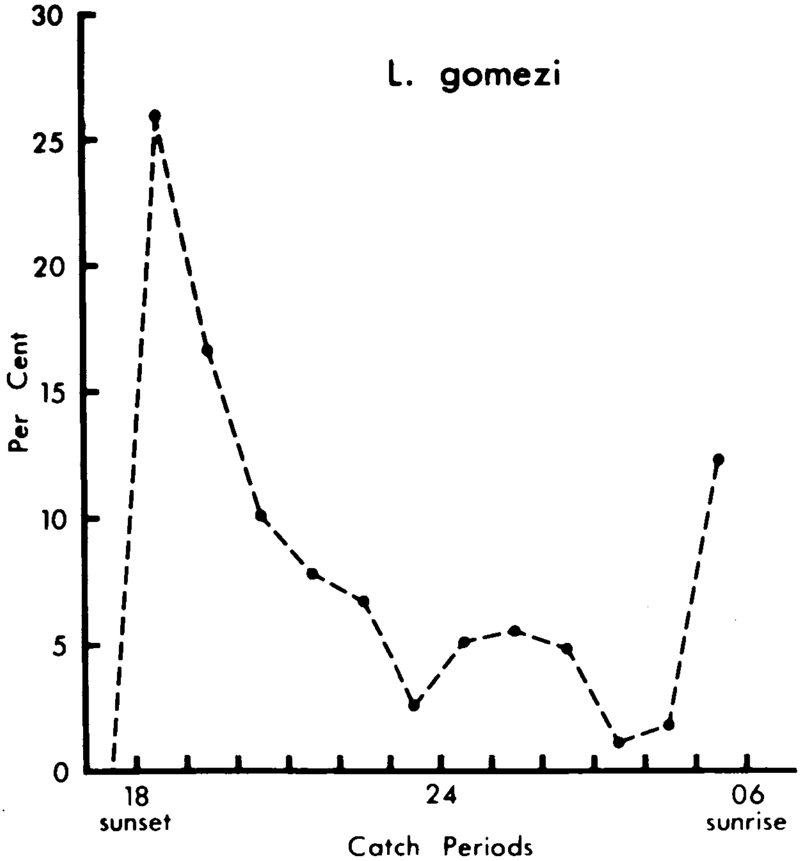

Fig. 23. Summary temporal pattern of man-biting activity at the clearing sites by *L. gomezi* based on modified geometric means converted to percentages. Each catch period approximates the corresponding hour as described in the text.

(Department of Valle). Young (1971) found this species in the Department of Chocó, Colombia. Most of his collections of this species were made in a mixed evergreen forest (Tropical Wet Forest Life Zone) about 0.5 km from the Pacific coast. Forattini and Galati (1977) have recently described the female of *L. ayrozai.* They determined that the female described and designated as allotype by Barretto and Coutinho (1943) was incorrectly associated and is actually *L. guyanensis* (Floch and Abonnenc).

The man-biting activity of *L. ayrozai* occurred almost exclusively at the Buenos Aires and Tiroteos forest sites (Tables 2 and 11). Unlike the Providencia site which was only about 40 m within the forest, both of these locations were at least 200 m from the forest margin. Since *L. ayrozai* was one of the predominant species in the light trap collections, the relatively low numbers of this species in the man-biting catches suggest that it was reluctant to bite man. A distinctive characteristic of this species' biting activity was its marked preference for the forest floor (Table 7). The biting activity of *L. ayrozai* tended to be concentrated between 1900 hours and midnight (Fig. 21). Although adults of *L. ayrozai* were taken throughout the entire year, the number of catches made was insufficient to reveal any distinct seasonal variations in its biting activity. Young (1971) collected the majority of his individuals of this species in June, biting man.

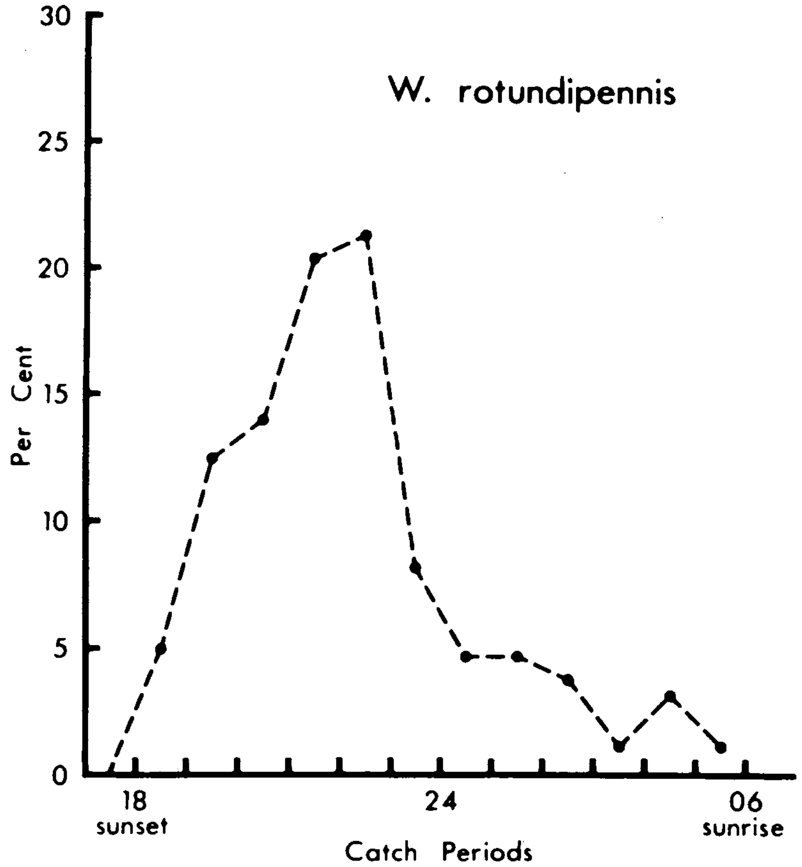

Fig. 24. Summary temporal pattern of man-biting activity at the clearing sites by *W. rotundipennis* based on modified geometric means converted to percentages. Each catch period approximates the corresponding hour as described in the text.

L. bifoliata Osorno-Mesa, Morales-Alarcón, F. de Osorno, and Muñoz de Hoyos, 1970

L. bifoliata is known only from Colombia and was described from a single male captured in the hollow of a tree at Puerto Boyacá, Department of Boyacá (Osorno-Mesa et al. 1970). The female has been illustrated by Young (1971) from specimens taken in the Providencia study area.

Although not abundant, *L. bifoliata* was taken primarily in the forest series of catches (Table 2). It was encountered most frequently at the Providencia and Tiroteos sites (Table 11). The biting activity of *L. bifoliata* occurred primarily in the canopy at the Providencia site but this preference was not apparent in the more open Tiroteos forest. The biting activity of *L. bifoliata* within the forest was primarily crepuscular; however, few individuals were encountered during the period preceding sunrise. Although adults of *L. bifoliata* were present during every month of the year, the number of catches made was insufficient to reveal any distinct seasonal variations in its biting activity. Adults were found to use the base of trees as a diurnal resting site. This was the second most numerous species encountered in a series of collections made from eleven tree bases over an eight month period. Its distribution however was rather localized as a mayority were taken from one tree.

L. gomezi (Nitzulescu), 1931

L. gomezi has a widespread geographic distribution, occurring from El Salvador and Nicaragua to Brazil, Peru, and French Guiana (Fairchild and Hertig 1959, Young 1971, and Llanos 1973). This species appears to be quite widely distributed in Colombia and has been taken primarily at elevations below 800 m (Barreto 1969, Young 1971, and Osorno-Mesa et al. 1972a). Fairchild and Hertig (1948) indicated that in Panamá this species bit man "both outdoors and in houses, even in quite urban areas... [and] it is probable that it is semidomestic."

A comparison of the modified geometric mean catches of *L. gomezi* for the forest and clearing habitats (Table 2) shows that the biting activity of this species was concentrated in the clearing. Although comparisons between the forest and clearing series of catches must be considered with some reservation, the difference appears to be of sufficient magnitude to indicate a definite preference by *L. gomezi* for the clearing habitat. In the forest catches, *L. gomezi* was taken almost exclusively at the Providencia site (94 of 95 individuals) which was only about 40 m away from the clearing site D. In the clearing *L. gomezi* was most numerous at site E which was at the edge of secondary forest and pasture. It was also quite common at sites F (edge of pioneer vegetation and pasture) and C (open pasture). Relatively small numbers of *L. gomezi* were encountered at site D which was at the edge of mature forest, and the difference in numbers taken between this site and site E was highly significant (Table 14). Young (1971) has noted that over most of its range this species tends to occur in cultivated or semicleared areas. Johnson et al. (1963) and Thatcher and Hertig (1966) found *L. gomezi* to be quite common in an area that was rapidly being cleared. Johnson et al. (1963) also found it to be one of the two predominant species attracted to man and horse in an area of mainly secondary growth. However, *L. gomezi* was not taken by Chaniotis and Correa (1974) in a small series of man-biting catches made in the center of a 27 x 33 m clearing.

At the Providencia platform site, *L. gomezi* was taken primarily in the canopy (Tables 5 and 7). Chaniotis et al. (1971b) obtained a similarly high percentage of man-biting activity by this species in the canopy relative to the forest floor. Johnson et al. (1963) also caught greater numbers of *L. gomezi* biting man at 11 m than at ground level. The limited study of the vertical distribution of phlebotomine sand flies by Ward et al. (1973) in the Serra dos Carajás, Pará State, Brazil, indicated that the biting activity of *L. gomezi* may also be primarily arboreal in that region. However, in an extensive series of light trap catches, Chaniotis et al. (1971a) obtained larger numbers of *L. gomezi* at ground level than in the canopy.

In the clearing habitat the man-biting activity of *L. gomezi* was primarily crepuscular (Fig. 23). A distinct peak in biting activity tended to occur between 1800 and 2000 hours, and there was an indication of a smaller peak from 0500 to 0700 hours. The biting activity of *L. gomezi* at the Providencia forest site (Table 22) was rather uniform throughout the night with only a slight indication of the distinctly crepuscular pattern observed in the clearing. The results presented by Chaniotis et al. (1971b) indicated that the man-biting activity of *L. gomezi* in the forest canopy was greatest at midnight and that there was very little biting at dusk.

There was an indication that the man-biting activity of *L. gomezi* was substantially reduced during the latter half of the rainy season, but due to the small sample size this could not be conclusively determined. In Panamá *L. gomezi* has been taken in greater numbers during the dry season than in the lengthier wet season from biting catches using man and horses (Johnson et al. 1963), from light trap collections (Chaniotis et al. 1971a), and from leaf litter, a diurnal resting site (Chaniotis et al. 1972). For the same area and period of time in which the aforementioned light trap collections were made, Chaniotis et al. (1971b) also carried out a series of man-biting catches which gave quite different monthly estimates of the population density of *L. gomezi*. These catches showed the man-biting activity of *L. gomezi* to be greatest at the end of the rainy season and the beginning of the dry season. Rutledge et al. (1975) have noted that for certain localities in the Panamá Canal Zone the *L. gomezi* - *L. panamensis* association of sand flies occurred in the relatively wet part of the year.

L. gomezi has been shown to feed on a variety of mammals (Thatcher and Hertig 1966, Thatcher 1968, Tesh et al. 1971 and 1972) and the domestic chicken (Thatcher and Hertig 1966). Johnson (1961) found that certain females of *L. gomezi* were autogenous and that reciprocal crosses with anautogenous individual failed to produce fertile eggs. In a study of diurnal resting sites, Chaniotis et al. (1972) found adults of *L. gomezi* primarily on the leaf litter of the forest floor, and it accounted for about 12% of the specimens taken from that microhabitat.

Johnson and Hertig (1961) have colonized *L. gomezi* and have determined the duration of the various developmental stages of the life cycle. These authors found that wild-caught females laid an average of 29 eggs and that the period of time from oviposition to adult emergence averaged about 34 days. Mirsa (1952) obtained rather similar estimates of the duration of the developmental stages of this species but found the average number of eggs per oviposition to be greater. Rutledge and Ellenwood (1975b and c) observed that the sites of larval development for *L. gomezi* were more abundant in hilltop regions and tended to be associated with large *Anacardium* trees.

Schneider and Hertig (1966) have shown one of the leptomonad infections isolated from *L. gomezi* by Johnson et al. (1963) to be a strain of *Leshmania braziliensis sensu lato.*

L. hartmanni (Fairchild and Herting), 1957

L. hartmanni appears to have a somewhat limited geographic distribution occurring in Panamá (Fairchild and Hertig 1957), Colombia (Barreto 1969), and Ecuador (D. G. Young, personal communication). This species has been taken at elevations varying from near sea level to at least 700 m. The known distribution of *L. hartmanni* indicates that it is primarily limited to forested areas in regions with high annual rainfall (Fairchild and Hertig 1957, Barreto 1969, and Young 1971). There is virtually no information in the literature about the man-biting activity of this species. *L. hartmanni* was encountered by Young (1971) in the series of man-biting catches he made in the Department of Chocó, Colombia. These catches, already described above, were made primarily at ground level. At the Curiche forest site which was adjacent to the Pacific coast, *L. hartmanni* accounted for 19% of the individuals taken; but at a somewhat drier site in an area of "semi-cleared primary forest" about 52 km inland, this species accounted for only 2% of the total catch.

The large numbers of *L. hartmanni* taken at all of the forest and clearing sites reflect this species' dominance of the man-biting activity in the Providencia area. Even though statistically significant differences were detected in the magnitudes of biting activity of *L. hartmanni* between the two edge sites and sites A and C within the clearing, it was still the most numerous species at sites A and C. The ubiquity of this species in both the forest and clearing habitats can perhaps be attributed to a rather broad microenvironmental tolerance enhanced by an optimal environment. A species occurring in an area which is environmentally optimal is thought to have a wider microenvironmental tolerance than it would have in a less favorable area where it would tend to be limited to those microenvironments most closely approximating the optimun. Thus, in an optimal environment a species may have increased niche space.

When summarized over sites, the man-biting activity of *L. hartmanni* was significantly greater in the canopy than either in the understory or on the ground. However, its pattern of vertical stratification varied extensively between the three forest sites (Table 5), and appeared to be influenced by forest structure. A significant difference in the magnitude of this species' biting activity between the canopy and ground levels was not detected at either the Buenos Aires or Tiroteos site. However at the Providencia site, where the biting activity of nearly all species was concentrated in the canopy, *L. hartmanni* was taken in significantly greater numbers in the canopy than that at ground level. Comparisons of biting activity across the three forest sites (Table 10) indicated that the magniof its activity in the understory was similar at all three sites. However, a significant difference was detected at ground level between the Buenos Aires site and the Providencia and Tiroteos site and in the canopy between the Tiroteos site and the Buenos Aires and Providencia sites. When the temporal pattern of this species' man-biting activity was differentiated by level, no distinct patterns of vertical movement were found. There was, however, a tendency for biting activity to be concentrated at ground level between 1900 and 0100 hours and in the canopy between 2100 and 0300 hours.

The temporal pattern of the man-biting activity of *L. hartmanni* was quite variable between nights at both the forest and clear ing sites. The individual night catches tended to have distinct but variable peaks in biting activiy. When summarized over sites and levels, biting activity tended to be concentrated in the forest between 1900 and 0300 hours and in the clearing between 1900 and 2300 hours. The magnitudes of biting activity from sunset through 2100 hours were similar fro both of the habitats but became substantially reduced in the clearing after that time. At the Buenos Aires site the biting activity of *L. hartmanni* tended to increase quite rapidly after sunset and to be concentrated between sunset and 0100 hours. At the other two forest sites, biting activity tended to increase at a more gradual rate after sunset and be concentrated over a somewhat later period of time. In the clearing, between-night variation in the temporal pattern of biting activity appeared to be somewhat dependent upon the site.

The monthly means presented in Table 23 suggest that seasonal changes in the biting activity of *L. hartmanni* in the Providencia region may be mild. Biting activity during the dry season may have been higher than usual due to an abnormally large rainfall for that period.

L. panamensis (Shannon), 1926

L. panamensis appears to be indigenous to forested lowland areas, elevations ranging from near sea level to about 800 m, from southern México and Belize to Colombia and Venezuela (Biagi and Biagi 1953, Fairchild and Hertig 1959, Williams 1965, and Osorno-Mesa et al. 1972). This species has also been reported from Brazil by Martins et al. 1963.

L. panamensis had rather similar magnitudes of biting activity both between and within the forest and clearing habitats. The modified geometric mean catches of this species for the forest and clearing habitats were almost the same (Table 2). The greater number of specimens taken at the Providencia site compared with the other two forest sites (Table 11) was due to a single large catch of 145 individuals on July 7, 1971. Significant differences in the magnitudes of biting activity were not detected between any of the clearing sites by the Scheffé pairwise contrasts (Table 14). However, the number taken and the modified geometric mean catch for each of the two edge sites were noticeably larger than those for sites A, B, C, and to a lesser degree, F (Table 13).

Whether *L. panamensis* has a distinct preference for the forest-clearing ecotone is difficult to ascertain from the literature. In Venezuela Pifano et al. (1960) captured large numbers of *L. panamensis* at the forest perimeter, especially in areas where trees were being cut. Both Pifano et al. (1960) and Scorza et al. (1968a) indicate that this species flies from the forest periphery at dusk to human dwellings. Our studies and those of Chaniotis and Correa (1974) show that *L. panamensis* is reluctant to enter clearings to bite man. However, as will become increasingly evident, the behavior of *L. panamensis* appears to be quite variable from one region to another.

L. panamensis is a common anthropophilic species in mature, disturbed, and secondary forest. In the Department of Chocó, Colombia, Young (1971) found that *L. panamensis* accounted for 44% of the evening (1830-2100 hours) ground level man-biting activity in a lowland forest (Tropical Wet Forest Life Zone) located less than a kilometer from the Pacific coast. This species accounted for 87% of the specimens taken in a similar series of catches made in a "semi-cleared primary forest" about 52 km inland and over approximately the same time period (April to December). However, in terms of actual numbers taken per man hour, *L. panamensis* was only about one-third as abundant at the latter site. On the basis of light trap collections, Chaniotis et al. (1971a) and Rutledge et al. (1976) found *L. panamensis* to be more abundant in mature forest than in adjacent secondary forest. In addition, Rutlege et al. (1976) found this species to be virtually absent from catches made within a cleared area adjoining secondary forest. Studies in a secondary forest by Johnson et al. (1963) revealed that *L. panamensis* was the predominant species attracted to man and horse during the rainy season. Ground level collections of phlebotomine sand flies using man as a bait were made at a number of forested areas in Belize by Williams (1965). In nearly all of the areas, *L. panamensis* was one of the dominant or subdominant species of the anthropophilic component. Disney (1968) indicates that the forests of Belize have been subjected to varying degrees of disturbance from both man and hurricanes.

The biting activity of *L. panamensis* for the three forest sites combined was declared to be significantly greater in the canopy than at either of the other two levels (Table 4). This pattern of vertical stratification was most apparent at the Buenos Aires and Providencia sites, but at the Tiroteos site biting activity was rather similar in magnitude at all three levels (Table 6). These patterns of vertical stratification differ markedly from those of previous studies where *L. panamensis* was found to bite primarily at ground level when either man (Fairchild and Hertig 1951, Johnson et al. 1963, Williams 1970a and b, and Chaniotis et al. 1971b) or animals (Disney 1968, and Thatcher 1968) were used as a bait. Williams (1970a and b) and Christensen et al. (1972) have compared light trap collections made near ground level with those made near or within the canopy. They obtained much larger numbers of *L. panamensis* in the proximity of the canopy than they did near the forest floor. However, in the extensive series of light trap collections made by Chaniotis et al. (1971a), approximately three times as many individuals of this species were taken near the ground as in the canopy. Disney (1968) found *L. panamensis* to be one of the predominant species occurring under dead leaves on the forest floor. Williams (1970b), however, suggests these may have been recently emerged flies and believes his light trap results may indicate that older individuals of this species commonly rest on the foliage of trees. Chaniotis et al. (1972) sampled a number of diurnal resting sites of phlebotomine sand flies in a Panamanian forest and found that. *L. panamensis* constituted about 10% of the individuals resting on the leaf litter of the forest floor and 1.5% of the individuals resting on green plants near the forest floor. Collections were also made from animal burrows and tree hollows and at varying heights on tree trunks, but few if any specimens of this species were obtained from these microhabitats.

The biting activity of *L. panamensis* within both the forest and clearing habitats (Fig. 14) tended to be concentrated in the interval from sunset to about 0200 hours. These patterns can be compared with those obtained by Williams (1966 and 1970b) for the ground level man-biting activity of this species in forested areas of Belize. In 1966, Williams reported on a short series of extended catches (each was 12-14 hours in duration) made at the end of a rainy season. The resulting temporal pattern showed a tendency for the man-biting activity of *L. panamensis* to be concentrated between 1800 and 2400 hours. Williams considered the pattern to be bimodal and speculated that such a pattern may be produced by variation in the time of biting activity of nulliparous and parous individuals. The results of a more extensive series of catches (Williams 1970b) indicated a distinctly bimodal pattern with a tendency for biting activity to be concentrated from 1700 to 0200 hours. The 1966 and 1970 temporal patterns were quite different from each other, suggesting that there may have been considerable between-night variation in the temporal pattern of biting activity. The temporal patterns presented by Williams (1966 and 1970b) also reveal that there was some diurnal biting activity, especially during the morning hours. *L. panamensis* was occasionally encountered in the diurnal series of forest catches at the Providencia study area (Table 8). Chaniotis et al. (1971b) also detected a small amount of diurnal biting activity by this species at ground level.

Seasonal variation in the man-biting activity of *L. panamensis* was very pronunced. Although this species was taken in the biting catches every month, it attained a distinct peak in biting activity during the rainy season months of June and July (Table 23). Fairchild and Hertig (1951) were perhaps the first to suggest that *L. panamensis* is primarily rainy season species. Since then several studies have shown this to be true (Biagi and Biagi 1953, Johnson et al. 1963, Disney 1968, Chaniotis et al. 1971a, Christensen et al. 1972, and Rutledge et al. 1976). The studies of Disney (1968) and Chaniotis et al (1971a) indicate that this species is most numerous during the first few months of the rainy season. The study by Chaniotis et al. (1971b) is an apparent exception as they found the man-biting activity of *L. panamensis* to be primarily concentrated in the dry season. Thus, the monthly estimates of the population density of *L. panamensis* derived from its man-biting activity (Chaniotis et al. 1971b) were quite dissimilar from those obtained for the same area by light traps (Chaniotis et al. 1971a).

L. panamensis appears to feed on a broad range of mammals (Thatcher 1968 and Tesh et al. 1972). Thatcher (1968) also found *L. panamensis* to be attracted to the domestic chicken.

Johnson and Hertig (1961) have determined for *L. panamensis* the length of time required to complete each of its developmental stages and found that the period of time from oviposition to adult emergence averaged about 28 days. In Venezuela, Mirsa (1952) observed the emergence of adults 29 days after oviposition. Wild-caught females were found to lay an average of 28 eggs by Johnson and Hertig (1961) while Mirsa (1952) obtained an average oviposition of 58 eggs from five wild females.

Hanson (1961) and Johnson and Hertig (1961) indicate that decaying leaves and litter in well-shaded areas on the forest floor are the sites of larval development for *L. panamensis*. Rutledge and Ellenwood (1975b and c) have shown that the forest litter and soil are modified by a variety of environmental factors which can influence the distribution of developing larvae. Thus "breeding populations" of *L. panamensis* were found to be greater in hilltop regions and to be associated with large *Anacardium tress*. Johnson and Hertig (1961) indicate that quiescence may occur in fourth-instar larvae of *L. panamensis* and is probably initiated by adverse conditions, especially a lack of moisture.

Christensen et al. (1969) isolated *Leishmania brasiliensis sensu lato* from a wild-caught *L. panamensis* and confirmed its identity through infection of hamsters. Promastigote (leptomonad) flagellates have been found in this species by Pifano (1940), Pifano et al. (1960), Johnson et al. (1963) and Williams (1970b). Johnson et al. (1963) found a comparatively low rate of leptomonad infection in wild-caught *L. panamensis*.

L. trapidoi.(Fairchild and Hertig), 1952

L. trapidoi has been found in Honduras, Costa Rica, Panamá, Ecuador (Fairchild and Hertig 1959), and Colombia (Barreto 1969). Its distribution resembles that of the Meso-American area of endemism of Martins and Morales-Farias (1972). This species has been recorded at elevations varying from near sea level to about 800 m (Fairchild and Hertig 1952, Barreto 1969, and Young 1971). Fairchild and Hertig (1952) indicated that in Panamá *L. trapidoi* occurred primarily in forested areas with high annual rainfall.

A distinctive characteristic of the man-biting activity of *L. trapidoi* in the Providencia study area was its strong preference for the canopy. At all three forest sites, a highly significant difference was detected in its biting activity between the canopy and the ground (Table 5). Highly significant differences were also detected between the canopy and the understory for the Buenos Aires and Providencia sites. The distinct concentration of this species' biting activity in the forest canopy was first noted by Fairchild and Hertig (1952) and was demonstrated quantitatively by Thatcher (1968) and Chaniotis et al. (1971b). Johnson et al. (1963) also found that *L. trapidoi* bit man in greater numbers on tree platforms than at ground level.

Chaniotis et al. (1974) hypothesized that *L. trapidoi* moves into the canopy at dusk from diurnal resting sites on or near the forest floor. This vertical movement was not detected by our catches. The summary temporal pattern of this species' biting activity partitioned by vertical level (Fig. 19) indicates that it was taken in greater numbers throughout the entire night in the canopy than at either of the other two levels. The infrequent diurnal biting activity of *L. trapidoi* occurred primarily in the understory.

The magnitudes of the man-biting activity of *L. trapidoi* at the three forest sites tended to vary with the vertical level. When a comparison was made between the sites of the biting activity for the first seven night catch periods, no statistically significant differences were detected for all levels combined. Since a considerable proportion of the biting activity of *L. trapidoi* frequently occurred after the first seven catch periods (Fig. 12), the pairwise contrasts (Table 10) should be considered with some caution. For individual levels, these contrasts did indicate that the biting activity of *L. trapidoi* in the canopy was significantly greater at the Providencia site than at the Tiroteos site. At ground level, biting activity was declared to be significantly greater at the Buenos Aires site than at either of the other two sites.

L. trapidoi bit man primarily in the forest canopy and was very reluctant to enter the clearing. The modified geometric mean catches for the two edge sites were, however, comparable with those for ground level at the Providencia and Tiroteos forest sites. *L. trapidoi* was rarely taken within the pasture (site C) or at the sites (A and B) furthest from mature forest.

Within the forest the biting activity of *L. trapidoi* tended to be concentrated between 2300 and 0500 hours. However, there was considerable between-night variation in the temporal pattern, and on many nights there was a distinct peak in biting activity. The limited biting activity at the clearing sites occurred primarily before midnight.

The biting activity of *L. trapidoi* tended to be quite variable from one month to the next, perhaps as a reflection of small sample size. However, there did not appear to be an appreciable decrease in activity during the unusually rainy dry season.

The diurnal resting sites of *L. trapidoi* in a Panamanian forest have been identified by Chaniotis et al. (1972). Although leaf litter on the forest floor was the preferred resting site, this species was also found to rest on green plants and tree trunks. Our collections from the base of large trees indicate that *L. trapidoi* rarely used this situation as a diurnal resting site in the Providencia study area.

L. trapidoi has been studied quite extensively in Panamá. Tesh et al. (1971 and 1972) showed by the precipitin test that this species feeds on a broad range of mammals and indicate that host selection is influenced by availability. *L. trapidoi* also is known to feed on birds (Thatcher and Hertig 1966 and Tesh et al. 1971). Johnson and Hertig (1961) reared *L. trapidoi* and determined the duration of its various developmental stages. Chaniotis (1975) described a different technique for rearing this species and reported on several aspects of its behavior in the laboratory. Chaniotis (1974a) also studied the sugar-feeding behavior of *L. trapidoi* in the laboratory. The sites of larval development have been investigated by Hanson (1961) and Rutledge and Ellenwood (1975a, b, and c).

L. trapidoi has been strongly implicated as a vector of cutaneous leishmaniasis (Johnson et al. 1962 and McConnell 1963), and in addition, a number of arboviruses have been isolated from this species (Tesh et al. 1974). Johnson et al. (1962) and McConnell (1963) have isolated leptomonad flagellates from wild-caught *L. trapidoi* which were subsequently shown to cause infections in the nose of hamsters similar to those produced by *Leishmania braziliensis sensu lato*. Johnson et al. (1963) obtained infection rates of promastigotes (leptomonads) as high as 15.4% for females of *L. trapidoi*, but with very few exceptions (McConnell 1963) they were not conclusively shown to be *Leishmania*.

L. yuilli (Young and Porter), 1972

L. yuilli appears to be near the northern limits of its range in the Providencia study area. This species has not been taken in Panamá or any of the other Central American countries but has been found in Pará State, Brazil (Lewis 1975), in the Departments of Cuzco and Huánuco in Peru (Llanos et al. 1975 and Martins et al. 1976), and in Ecuador and Surinam (D.G.Young, personal communication). In Colombia *L. yuilli* has also been collected near Caucasia, Department of Antioquia and Tres Esquinas, Department of Caquetá (D.G. Young, personal communication).

L. yuilli was observed to be primarily a forest species. The modified geometric mean catch of this species for the Buenos Aires forest was almost three times as large as the corresponding mean catch for the Tiroteos forest which had been subjected to some selective cutting. For all levels combined a highly significant difference was detected in the biting activity of *L. yuilli* between the Buenos Aires site and each of the other two forest sites (Table 10). The difference between the Buenos Aires and Providencia sites was due to the very reduced biting activity in the understory and on the forest floor at the Providencia site, while the difference between the Buenos Aires and Tiroteos sites was primarily the result of diminished biting activity in the canopy at the Tiroteos site. In the clearing the biting activity of *L. yuilli* was greatest at site E (Table 13) which was located at the edge of early secondary forest and pasture. This species was taken in smaller numbers at sites D (edge of mature forest and pasture) and F (edge of pioneer vegetation and pasture) and was seldom encountered at site C (open pasture) and sites A and B which were over 200 m from mature forest. The large number of specimens taken at site E was primarily the result of a very large catch at this site in March. A total of 29 individuals of *L. yuilli* were taken at this site during the remaining five catches whereas 39 were taken at site D. Thus in the clearing habitat the biting activity of *L. yuilli* was concentrated at the forest margin. Some biting also occurred in the pioneer vegetation which extended from the forest; however, this species appeared reluctant to extend very far into the clearing, even along the pioneer vegetation.

For the three forest sites combined, a highly significant difference was detected in the man-biting activity of *L. yuilli* between the canopy and each of the other two levels (Table 4). However, the vertical stratification of this species' biting activity appeared to be particularly influenced by forest structure. At the Providencia site where the upper canopy was quite dense, the biting activity of *L. yuilli* occurred primarily in the canopy (Table 6) while in the relatively open Tiroteos forest, a significant difference was not detected between any of the levels (Table 5).

Although the summary temporal pattern of the biting activity of *L. yuilli* for the forest catches appears to be somewhat bimodal (Fig. 13), the patterns for the individual nights were quite variable. On many of the nights, there was a sudden, pronounced surge in biting activity during one or occasionally two catch periods, and these surges tended to be quite variable with respect to time (Fig. 20). The biting activity of *L. yuilli* at the clearing sites tended to be concentrated between 0800 and 2200 hours (Fig. 13).

L. yuilli was taken in the forest man-biting catches throughout the entire year. Seasonal variations in its biting activity are difficult to determine from this study, although there is an indication that its activity may have increased during February, March, and April. February and March are the last two months of the dry season. Adults of *L. yuilli* did not use the base of large trees as a diurnal resting site.

W. rotundipennis (Fairchild and Hertig), 1951

W. rotundipennis has been found in Costa Rica, Panamá, and Colombia (Fairchld and Hertig 1959 and Young and Chaniotis 1972) at elevations ranging from 35 m (Young 1971) to 690 m.

The man-biting activity of *W. rotundipennis* was greatest in the clearing habitat where it was taken in rather similar magnitudes at both exposed and edge locations. The modified geometric mean catch for the clearing habitat was considerably larger than that for the forest (Table 2). As mentioned earlier, comparisons between the forest and clearing series of catches should be made with caution, especially since the clearing catches were only made over a 6-month period. No statistically significant differences were detected in the biting activity of *W. rotundipennis* between the six clearing sites (Table 14).

In the forest catches, *W. rotundipennis* was taken primarily at the Providencia site (84 of 88 individuals). The modified geometric mean catches for the three vertical levels at the Providencia platform site (Table 7) were to varying degrees less than those for the clearing sites with the exception of site A (Table 13).

No significant difference was detected in the man-biting activity of *W. rotundipennis* between the three vertical levels at the Providencia platform site (Table 5). *W. rotundipennis* was the only species regularly taken at the Providencia site which did not have a strong preference for the canopy at this location. The canopy preference was so pronounced in the other species that *W. rotundipennis* was the second most frequently encountered species on the forest floor at this site.

At the clearing sites the man-biting activity of *W. rotundipennis* tended to be concentrated between 1900 and 2400 hours (Fig. 24). The temporal distribution of those individuals of this species taken in the forest catches is given in Table 22. There was very little biting activity in the forest before 2000 hours. Adults of *W. rotundipennis* were present throughout the year; however, there was an insufficient number of catches to ascertain seasonal trends.

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APPENDIX

Checklist of Phlebotomine Sand flies of the Providencia Region[a]

Brumptomyia leopoldi (Rodriguez), 1953
Lutzomyia abonnenci (Floch and Chassignet), 1947
L. aclydifera (Fairchild and Hertig), 1952
L. aragaoi (Costa Lima), 1932
L. ayrozai (Barretto and Coutinho), 1940
L. barrettoi (Mangabeira), 1942
L. bifoliata (Osorno-Mesa, Morales-Alarcón de Osorno, and Muñoz de Hoyos), 1970
L. camposi (Rodriguez), 1950
L. caprina Osorno-Mesa, Morales-Alarcón and Osorno, 1972
L. carpenteri (Fairchild and Hertig), 1953
L. cirrita (Young and Porter), 1974
L. dasymera (Fairchild and Hertig), 1961
L. gomezi (Nitzulescu), 1931
L. hartmanni (Fairchild and Hertig), 1957
L. micropyga (Mangabeira), 1942
L. nocticola (Young), 1973
L. nordestina (Mangabeira), 1942

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[a] Based on identifications made by D. G. Young, Department of Entomology, University of Florida.

L. olmeca-bicolor (Fairchild and Theodor), 1971
L. sp. near osornoi (Ristorcelli and Van Ty), 1941
L. panamensis (Shannon), 1926
L. pessoana (Barretto), 1955
L. pilosa (Damasceno and Causey), 1944
L. rorotaensis (Floch and Abonnenc), 1944
L. runoides (Fairchild and Hertig), 1953
L. saulensis (Floch and Abonnenc), 1944
L. serrana (Damasceno and Arouck), 1949
L. shannoni (Dyar), 1929
L. spinosa (Floch and Abonnenc), 1942
L. trapidoi (Fairchild and Hertig), 1952
L. trinidadensis (Newstead), 1922
L. triramula (Fairchild and Hertig), 1952
L. tuberculata (Mangabeira), 1941
L. vespertilionis (Fairchild and Hertig), 1947
L. yuilli (Young and Porter), 1972
L. sp. N (verrucarum group)
L. sp. N (ungrouped)
Warileya rotundipennis (Fairchild and Hertig), 1951

Addendum

Since the submission of this paper for publication, a major work on the classification of Colombia Phlebotominae has been published by Dr. David G. Young.[a] The species which we have called *Lutzomyia* sp. near *osornoi* (Ristorcelli and Van Ty), 1941, is now recognized by Young as a distinct species, i. e., *Lutzomyia strictivilla* Young, 1979.

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[a] **David G. Young, 1979. A Review of the Bloodsucking** Psychodid Flies of Colombia (Diptera: Phlebotominae and Sycoracinae). Agricultural Experiment Stations Bulletin. 806 (technical), University of Florida, Gainesville, Florida. 266 pp.