Mem. Inst. Oswaldo Cruz, Rio de Janeiro, Vol. 82 (1) :125-131, jan./mar. 1987

ECOLOGY OF SANDFLIES (DIPTERA: PSYCHODIDAE) IN A RESTRICTED FOCUS OF CUTANEOUS LEISHMANIASIS IN NORTHERN VENEZUELA. II. SPECIES COMPOSITION IN RELATION TO HABITAT, CATCHING METHOD AND HOUR OF CATCHING

M. DORA FELICIANGELI
Centro de Investigaciones Biomédicas, Facultad de Ciencias de L. Salud, Universidad de Carabobo
Núcleo Aragua, Apartado 4944 Maracay, Venezuela

The ecology of phlebotomine sandflies in an endemic focus of cutaneous leishmaniasis in Northern Venezuela (San Esteban, Carabobo State) was investigated through a year-term study. Three different habitats: viz. a house, a peridomestic area and a sylvatic area, were covered and the species composition, the abundance and occurrence of each species were analyzed in relation to the habitats, catching methods and hour of catching.

L. panamensis, L. gomezi *and* L. ovallesi *are the species which bite man, although almost exclusively at night. All of them hide by day and are common in the sylvatic area. Moreover,* L. panamensis *and* L. gomezi *successfully approach the house and seem to settle in the peridomestic area.* L. shannoni *and* L. olmeca bicolor *also approach and accidentally bite man.* L. trinidadensis, L. atroclavata *and* L. cayennensis *are the common non-anthropophilic species in the area.*

Key words: ecology of sandflies – cutaneous leishmaniasis – northern Venezuela – catching methods – hour of catching

In order to gather the threads of "where, when and how the transmission occurs" and which species of sandflies may be responsible for the cutaneous leishmaniasis incidence in a small village in Northern Venezuela, San Esteban, a study on the ecology of phlebotomine sandfly fauna was carried out in three different habitats: viz. a house, a peridomestic area and a sylvatic area. For a better understanding of the total phlebotomine population, several collecting methods were used since no single trapping technique would catch all species present in any one area. In fact even if several species were caught by one method, it is highly unlikely that they would be equally sampled.

This paper deals with the adult population features of species collected, and their relation with the habitats, capture methods and time of capture.

MATERIALS AND METHODS

The study area and the catching methods have been previously described (Feliciangeli, 1987). Briefly, searches in domestic resting sites (internal and external walls and household goods), peridomestic and sylvatic resting sites (aerial roots, trunks, shaded crevices), direct human and animal (pig and cow) bait catches were performed weekly in the morning (08:00 - 11:00 hrs) or at night (19:00 - 22:00 hrs) alternately during one year. Additionally, light traps (Shannon trap and CDC trap) were used during nightly collections.

Statistical methods – The counts of sandflies has been analyzed using Genstat, a statistical package developed at Rothampstead Experimental Station (Alvey et al., 1977). The programs are available from the Department of Pure and Applied Biology, Imperial College, London, U. K.

An analysis of Deviance (multi way tests with any number of factors) was carried out to the counts of sandflies. The basic approach of Linear Modelling with Genstat is that one calculates expected frequencies of sandflies, and from this calculates the value of χ^2. This is called the Deviance and is analogue to the variance of normal statistics. In this analysis one fits factors in turn and measures the reduction in χ^2, or the amount of Deviance which each factor explains. Since the mean deviance is a measure of the change in χ^2 per degree of freedom, so it allows different factors to be compared fairly directly only. This value and the probability level will be given in the results. The higher mean deviance value of a factor, the higher its contribution to the total variation observed.

In view of some involuntary omissions, for example a pig was available only eight months, while a cow was available for only four, and also that there were no day time collections from the two light traps or from the cow and

This investigation was financed in part by the UNDP/World Bank/WHO Special Programme for Research and Training in Tropical Diseases (Project 790192) and formed part of a thesis approved for the Ph.D. degree at the University of London.
Received July 11, 1986.
Accepted December 29, 1986.

pig collections, the statistical analysis for each species was divided in this paper in two sections: *Section A.* Was restricted to the first six types of collections, i.e. from walls, trees and from human in each of the three habitats. All collections from the 13th month were excluded. This allowed a comparison between the three habitats, and it identified those sandflies which bit or congragated near humans.

Only female sandflies bite, so the catches of males and females were analyzed separately and classified according to four other factors: *Hour* (day or night), *Habitat* (house, peridomestic area or sylvatic area), *Method* (methods used both day and night) and *Month*. The interaction among pairs of factors was analyzed. *Section B.* Was restricted to the four months (July, August, September and October) in which a cow was available and to night time catches. This allowed all the methods to be compared without omitted collections.

In the previous paper, the sandfly species collected were classified, according to the relative occurrence, as common species: *L. panamensis, L. ovallesi, L. gomezi, L. trinidadensis, L. atroclavata, L. cayennensis, L. shannoni* and *L. olmeca bicolor* and rare species: *L. punctigeniculata, L. rangeliana, L. evansi, L. dubitans* and *Brumptomya* sp.

Samples of rare species were too small to justify a statistical analysis and this was done only with common species.

RESULTS

Species composition in relation to the habitats – All species were collected at the field site, which is probably related to the sylvatic origin of Neotropical sandflies. Eight of thirteen species (61.5%) were encountered in the peridomestic habitat and seven of thirteen (53.8%) in the house. The average number of insects of these species caught with the same methods in the neighbourhood of the house was higher than at the field site (Tables I & II).

Composition in relation to capture methods – Catching methods were not used uniformly during the period of study: a constant sampling time of 3 hours had been initially planned but several problems prevented this regime from bein maintained. For instance the exploration of the house had to be delayed sometimes because of the locked doors. Though late starts could be compensated for by late finishes, the catch was different because of the hourly fluctuations in the activities of sandflies. Collection times using human bait were affected by the density of sandflies: at times so many flies were feeding that the men found it impossible to remain still and some flies were disturbed. Several times sudden rain forced the removal of a Shannon trap and the interruption of the catch. In order to make the results comparable, the numbers of sandflies collected were divided both by the time employed and number of collectors and is expressed as number of sandflies/man/hour. For the Shannon trap, the time of exposure of the trap, the time of collection and the number of collectors were taken in consideration.

The occurrence and abundance of sandflies in relation to capture methods is directly related to specific habits (Tables I, II). Collections from human bait detected three anthropophilic species: *L. panamensis, L. ovallesi* and *L. gomezi*. They were encountered attacking man in all habitats but were found rarely on trees and, when present, were always in low numbers.

Collections in trees were especially successful for non-anthropophilic species: *L. trinidadensis, L. atroclavata* and *L. cayennensis*, frequently associated inhabitants of tree holes. *L. shannoni* was found with a relatively low frequency and low density on trees and then only in the peridomestic habitat.

All anthropophilic species were attracted by pig and cow. While the number of *L. ovallesi* caught on pig was similar to that caught on man, many more *L. gomezi* and *L. panamensis* were caught on the pig than on human bait.

Light traps proved to be the most efficient method of capture since 86.6% of all species were trapped by Shannon and CDC traps combined. The Shannon trap gave better results than CDC traps in terms of number and density of species trapped except for *L. trinidadensis* and *L. cayennensis.* Both these species are known not to be phototropic. The numbers of *L. panamensis* attracted by light was overwhelming in relation to all other species. Although *L. ovallesi* and *L. gomezi* were regularly trapped by light traps they were always in low numbers. *L. o. bicolor*, a species thought not to be abundant, was caught several times in light traps.

Composition in relation to the time of capture (Tables I &II) – Anthropophilic sandflies usually, but not always, feed at night or during the few hours of twilight before sunset and after sunrise. The crepuscular and nocturnal biting activity was seen in the present study, human bait being more freqüently attacked at night than in daylight. In contrast more sandflies were aspirated from trees during the day than at night. Males predominated in tree catches from the peridomestic area at day and night, and from the field site during the day. Curiously, more females than males were caught from the field at night.

TABLE I

Female sandflies/man/hour ($\bar{x}$) caught at day time by habitat and collecting method (San Esteban, Venezuela, March 1979-1980)

Species	House		Peridomestic area		Sylvatic area	
	Walls	Biting man	Trees	Biting man	Trees	Biting man
L. atroclavata	0.06	--	0.33	--	0.24	--
L. cayennensis	0.19	--	0.56	--	0.08	--
L. gomezi	--	--	0.03	--	0.06	--
L. ovallesi	--	--	--	--	0.11	0.05
L. panamensis	0.06	--	0.64	0.06	--	0.13
L. shannoni	--	--	0.08	--	--	--
L. trinidadensis	0.12	--	3.77	--	8.49	--

TABLE II

Female sandflies/man/hour ($\bar{x}$) caught at night by habitat and collecting method (San Esteban, Venezuela, March 1979 – 1980)

Species	House			Peridomestic area				Sylvatic area		
				Biting						
	Walls	Biting Man	Trees	Man	Pig	Cow	Trees	Biting Man	Shannon trap	CDC trap
L. atroclavata	--	--	0.12	--	--	--	0.05	--	0.04	0.03
L. cayennensis	--	--	0.32	0.06	--	--	0.09	--	--	0.06
L. dubitans	--	--	--	--	--	--	--	--	--	0.04
l. gomezi	0.28	0.38	--	3.24	15.25	3	0.18	2.68	1.98	1.85
L. o. bicilor	--	0.07	--	--	--	--	--	--	0.24	0.09
L. ovallesi	--	0.31	0.09	0.71	1	--	0.07	16.93	6.63	1.58
L. panamensis	3.57	4.17	0.42	17.38	58.0	143.5	5.17	20.58	72.42	56.67
L. shannoni	--	--	0.25	--	0.25	--	--	0.07	0.09	--
L. trinidadensis	0.06	0.08	1.48	--	--	--	3.46	--	0.05	0.09
Brumptomyia sp.	--	--	--	--	--	--	--	--	0.007	--

TABLE III

Analysis of deviance: Degrees of freedom, mean deviances and significance levels for "common" species of sandflies at San Esteban, Venezuela

Section A Factor	DF	*L. panamensis*	*L. ovallesi*	*L. gomezi*	*L. o. bicolor*	*L. shannoni*	*L. trinidadensis*	*L. atroclavata*	*L. cayennensis*
Hour	1	1652.8***	718.27***	233.96***	3.07--	4.75*	107.30***	7.99**	5.19*
Habitat	2	111.4***	440.52***	27.81**	2.18--	7.05**	187.10***	5.55**	13.83**
Method	1	408.6***	612.33***	151.78***	2.91--	4.27*	580.40***	34.99**	34.04**
Month	11	65.2***	128.50***	9.36***	0.62--	2.53**	3.55**	0.96--	2.82**
Hour Habitat	2	16.4**	0.37--	0.56--	0.00--	0.61--	2.15--	1.23--	2.07--
Hour Method	1	46.1***	24.14***	16.41**	0.01--	1.36--	3.08--	0.00--	5.75**
Hour Month	11	7.0**	4.48**	1.28--	0.00--	0.17--	7.16**	1.05--	1.88**
Habitar Method	2	67.0***	1.95--	11.30**	0.00--	4.89**	4.25*	0.00--	0.58--
Habitat Month	22	9.0***	4.18**	2.98**	0.00--	0.37--	2.31**	0.99--	1.28--
Method Month	11	12.1***	7.37**	2.68**	0.00--	0.89--	0.40--	0.00--	0.41--
Section B Method	9	162.32***	1.99*	18.37***	0.44--	1.82--	11.33***	1.24--	1.45--

***P $<$ 0.001 **P $<$ 0.01 * P $<$ 0.05 -- No significant

Analysis of deviance – This is sumarized in Table III: the mean deviance by each studied factor (habitat, method, hour, month) and the interaction between pair of factors is given with their significance level, for all the common species. For *L. panamensis*, the anthropophilic species of highest abundance and occurrence, all four factors had a significant effect on catching rate, as did all the two-way interactions. In some species the interactions were not significant, which means that the main effects alone and independently were responsible for the results, i. e. *L. ovallesi* catches were not influenced by the interaction of method and habitat: although this species was a very good man biter in the sylvatic area, it appeared as a bad biter in the house (Table II). In biological terms this observation would be easily interpreted as a result of the fact that the species is sylvatic and it does not approach the house in high densities. The high levels of statistical significance in *L. panamensis* are due principally to the large numbers caught and with such numbers it is possible that weak effects with little biological importance are statistically very significant. On the other hand, although *L. o. bicolor* did not score significant levels because of the scarce numbers collected, the fact it was encountered into the house and biting man in several occasions, has to be taken in account because of its epidemiollogical significance.

DISCUSSION

Specific features in relation to the habitat. Significant statistical differences were found between the size of the sandfly population in the three habitats explored (Table III).

Seven species of sandflies were found at San Esteban in the house: three *(L. panamensis, L. gomezi* and *L. ovallesi)* were classified as anthropophilic because they were regularly collected biting man. *L. trinidadensis, L. atroclavata* and *L. cayennensis* were classified as non-anthropophilic species since they were mainly found resting on walls and in shelters and only occasionally both sexes were caught alighting on man. *L. o. bicolor* was collected biting man in the house as well in the sylvatic site. However, this species is considered weakly anthropophilic.

Flies may enter houses either in search of food or as a result of positive phototaxis. It is unlikely that the three non-anthropophilic species were attracted by light, since they were not frequently caught by the two light traps. The poor attraction of *L. trinidadensis* to light has been noticed also by Chaniotis et al. (1971a) and Christensen, et al. (1972). On the other hand, *L. atroclavata* never alighted on man and only one male of *L. cayennensis* and one female of *L. trinidadensis* were caught on man during a year of collection. This was in agreement with the observations in the peridomestic and in field habitats. Williams (1970) reported similarly low numbers of *L. trinidadensis* on man in Belize and Tesh et al. (1971) found that 76% of blood meals of *L. trinidadensis* reacted with reptile-amphibian antisera, confirming the general belief that *L. trinidadensis* is a saurophilic species (Ortiz, 1968; Forattini, 1973; Young, 1979). It is likely that *L. trinidadensis, L. atroclavata* and *L. cayennensis* enter houses in search of geckos and other small lizards which abound in the cracked walls of the rural houses. However Scorza et al. (1979) and Zeledón et al. (1982) recently pointed out that *L. trinidadensis* can have a wider range of hosts, including man. The finding of *L. panamensis* in houses is presumably the result of both positive phototaxis and anthropophily. This is indicated by high number of flies caught both in light traps and biting man in peridomestic and field habitats. *L. gomezi* and *L. ovallesi* probably only enter human dwelling in search of bloodmeals since they show little if any phototaxis. The number of these species attracted to light traps in sylvatic places was low in comparison with the population attracted to man. In contrast, though of low overall abundance, many more specimens of *L. o. bicolor* were caught in light traps than biting man and they probably enter the houses as a result of phototaxis alone. They show no marked anthropophily and possible bite man only when accidental contact. First observations on the behaviour of *L. o. bicolor* at Sasardí (Panamá) (Fairchild & Theodor, 1971) showed that it was similar to that observed at San Esteban. Later it was indicated as the dominant species collected in forest from litter and in rodent-bited castor oil traps (Christensen et al., 1972). In Colombia, Providencia, *L. o. bicolor* was rarely found biting man (Porter & De Foliart, 1981).

Tree searches in the peridomestic area showed that *L. atroclavata, L. cayennensis and L. shannoni* tend to concentrate in this habitat. *L. shannoni*, which was very abundant in trees in Belize (Williams, 1970) in Panamá (Chaniotis et al., 1971a; Christensen, et al., 1972) and in Colombia (Porter & De Foliart, 1981) was very poorly represented in San Esteban. The paucity of the anthropophilic species found in trees in the present study has also been observed in Belize (Williams, 1970); Panamá (Chaniotis, et al., 1971 a) and in Brazil (Ward et al., 1973). The resting sites of these species still remain an enigma. Though Rutledge et al. (1976) suggested that *L. panamensis* rested in tree trunks, in tree hollows, green plants and forest litter, the number caught in such sites seems too small to indicate a general trend.

Their presence in the peridomestic area was mainly detected by human and animal baits. *L. gomezi* was caught in larger numbers in the peridomestic habitat than in the house and in the field area indicating a definite preference for sites cleared of vegetation. This result agrees with the observation of Fairchild & Hertig (1948) who defined this species as "probably semidomestic" having found it biting man "both outdoors and in houses, even in quiet urban areas" in Panamá. Johnson & Hertig (1961) and Thatcher & Hertig (1966) found this species to be very common in an area of secondary growth. Another relevant feature of this species in the peridomestic habitat is the predominance of males in all the catches, especially on the hosts. 17 females were caught probing or feeding and 32 males were caught ' dancing" on man by Miles et al. (1976) in Panamá. At San Esteban the males were caught landing on the host and their presence in such large numbers must be another example of mating aggregation as indicating by Miles, et al. (1976). This phenomenon was also observed in *L. shannoni* attracted to man, pig and cow. A similar observation for this species was also reported by Miles, et al. (1976) and Williams (1970). This last author also recorded *L. shannoni* as the third most abundant man-biting species after *L. cruciata* and *L. panamensis*. Moreover only a few man-biting *L. shannoni* were caught in Panamá (Chaniotis et al., 1971 a, b), in Brazil (Ward et al., 1973), at Curiche, Colombia (Young, 1979) and at Providencia, Colombia (Porter & De Foliart, 1981). Because of the low relative occurrence of female *L. shannoni* biting man, this species was not considered to be truly anthropophilic at San Esteban.

The predominant species in the sylvatic area were the non-anthropophilic *L. trinidadensis* and the anthropophilic *L. panamensis* and *L. ovallesi*. *L. panamensis*, a successful species ranging from southern Mexico, through Belize, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Peru and Brazil (Martins, et al., 1978) has been demonstrated as highly anthropophilic in mature, disturbed and secondary forest (Porter & De Foliart, 1981). At San Esteban it attacked man in similar numbers in the forest and in the peridomestic habitats. Though Porter & De Foliart (1981) considered that the fly's behaviour varies with the area, Rutledge et al. (1976) found this species to be virtually absent from catches made within a clearing. In contrast *L. ovallesi* is without doubt a sylvatic species which probably strays into houses and the peridomestic habitat in search of a blood-meal. The distribution of this species is limited to Central America and Northern South America (Martins et al., 1978). Its behaviour seems to be variable. In Panamá Chaniotis et al. (1971a, b) never caught *L. ovallesi* biting man although densities in trees were appreciable. In contrast, it was caught on man in Colombia and British Honduras (Osorno-Mesa et al., 1972, Williams, 1970). In Venezuela it is also considered to be decidely anthropophilic with a wide distribution between altitude of 100 to 1800m (Mogollón et al., 1977).

Specific features in relation to capture methods – A comparison was made between all the collection methods during the months in wich domestic animals were used as bait. This showed that certain methods were more efficient at catching flies and that these varied with the species of fly. The differences were statistically significant for almost all the common species (Table III). The efficiency of each method was dependent on the behaviour and activity of the sandflies. The results from the comparison have already been partly discussed in relation to the three collection habitats.

As previously observed (Chaniotis et al., 1971a), light traps proved to be a useful and reliable collecting method for surveying the phlebotomine fauna since they attracted most of the species present in the study area.

Results from animal-baits were of particular interest. The attraction of *L. panamensis* to man, pig and cow seems to be of similar intensity. Though there were differences, e.g, more flies biting cow than pig and more biting pig than man, these may be the result of differences in surface area of hosts, rather than difference in "actractiveness". The behaviour of *L. ovallesi* was different from *L. gomezi*. Both attacked pig more than man but *L. ovallesi* did not bite cow at all whereas *L. gomezi* attacked the cow about as often as man. These anthropophilic sandflies are probably often diverted from entering houses and attacking man by the attraction of domestic animals in the neighbourhood. Zooprophilaxis might therefore be one method of reducing man-fly contact in endemic foci of leishmaniases in which sandflies show a similar behaviour.

Specific features in relation to the time of capture – The comparison of results of catching at different hours, showed higly significant differences for all the common species at San Esteban except *L. o. bicolor* (Table III).

Most of the non-anthropophilic species found in their resting sites were collected during morning hours and there was very little diurnal man-biting activity of anthropophilic sandflies Nevertheless a few *L. panamensis* were seen to be active in daylight in all the habitats and *L. ovallesi* was occasinally found attacking man in the field site during the morn-

ing. Porter & De Foliart (1981) observed a low level of diurnal activity of anthropophilic species at Prividencia, Colombia. They thought this was because there was no avid man biting species with a distinct preference in the forest floor where they are easily disturbed by man. However at San Esteban such an avid feeder does exist in the form of *L. panamensis*, the breeding sites of which are thought to be decaying leaves and forest litter (Hanson, 1961; Johnson & Hertig, 1961; Rutledge & Ellenwood, 1975 a, b, c). The man bait is possibly less likely to be attacked when motionless on a chair that when walking. Movement may stimulate flies resting on nearby ground vegetation to attack and feed as Williams (1970) observed with *L. o. olmeca* (Vargas & Diaz-Najera, 1959). However, Ward et al. (1977) found no evidence of increasing man-biting activity of *L. flaviscutellata* when vegetation was disturbed at dawn. Another explanation is simply that an upright man may be more attractive than a seated one. However, Shaw et al. (1972) found that seated bait caught more *L. flaviscutellata* than upright bait. Even if Fraiha, et al. (1971) reported a high activity of *L. wellcomei* (Fraiha et al., 1971) throughout the day and night, it is likely that diurnal attacks are atypical and accidental for the majority of sandflies and the typical behaviour is to feed between dusk and dawn.

On the whole, it is possible to provide a thumb-nail sketch of the ecology of phlebotomine sandflies at San Esteban: *L. panamensis, L. gomezi* and *L. ovallesi* are the species which definitely bite man, although almost exclusively at night. All them hide by day and are common in the sylvatic area. Moreover, *L. panamensis* and *L. gomezi* successfully approach the house, and seem to settle in the peridomestic area. *L. shannoni* and *L. o. bicolor* also approach and accidentally bite man. *L. trinidadensis, L. atroclavata* and *L. cayennensis* are the common non-anthropophilic species in the area while the remaining components of the sandfly fauna, *L. punctigeniculata, L. rangeliana, L. evansi* and *L. dubitans* might be considered as rare species.

RESUMO

Foi realizado um estudo ecológico dos flebótomos em um foco endêmico de leishmaniose cutânea na Venezuela a partir de observações em três ambientes: doméstico, peridoméstico e silvestre, durante o período de um ano.

Foram analisadas a composição, a abundância e a ocorrência de cada espécie em relação ao ambiente, ao método e horário de captura.

As espécies *L. panamensis, L. gomezi* e *L. ovallesi* são as que picam o homem, apesar de quase que exclusivamente durante a noite, escondendo-se durante o dia, e são comumente encontradas em áreas silvestres. Além disso, as espécies *L. panamensis* e *L. gomezi* se aproximam das casas e aparentemente se estabelecem na área peridoméstica.

As espécies *L. shannoni* e *L. olmeca bicolor* também se aproximam das casas e acidentalmente picam o homem. Já as espécies *L. trinidadensis, L. atroclavata* e *L. cayennensis* que geralmente não são antropofílicas, são comuns nesta área.

Palavras-chave: ecologia de flebótomos – leishmaniose tegumentar – norte da Venezuela – métodos de captura – horário de captura

ACKNOWLEDGMENTS

I wish to thank Prof. L. Deane (Instituto Oswaldo Cruz) for his invaluable orientation in this study and to Dr. R. Killick-Kendrick (University of London, Imperial College of Science and Technology) for his critical and helpful discussions on the work. I also wish to express my gratitude to Dr. K. R. Wallbanks (University of London, Imperial College of Science and Technology) and Dr. A. Montagne (Universidad Central de Venezuela) for their help during the writing of the original and final manuscripts respectively. Special thanks are due to Dr. A. Ludlow (University of London, Imperial College of Science and Technology) who developed the statistical analysis and wrote the Genstat programs. I also thank Mrs. R. Ordoñez, Mr. E. Fernandez, Mr. A. Bravo and Mr. F. Arias (Universidad de Carabobo) for their technical assistance. I am grateful to Dr. H. Malavé, Chief of the Division of Malariology for providing human and material assistance for this work.

REFERENCES

ALVEY, N. G.; BANFIELD, C. F.; BAXTER, R. I.; GOWER, J. C.; KRZANOWSKI, W. J.; LANE, P. W.; LEECH, P. K.; NELDER, J. A.; PAYNE, R. W.; PHELPS, K. M.; ROGERS, C. E.; ROSS, G. J. S.; SIMPSON, H. R.; TODD, A. D.; WEDDERBURN, R. W. M. & WILKINSON, G. N., 1977. Genstat. A General Statistical Program. Rothamsted Experimental Station.

CHANIOTIS, B. N.; NEELY, J. M.; CORREA, M. A.; TESH, R. B. & JOHNSON, K. M., 1971a. Natural population dynamics of phlebotomine sandflies in a Panamanian rain forest. *J. Med. Entomol., 11:* 369-375.

CHANIOTIS, B. N.; CORREA, M. A.; TESH, R. H. & JOHNSON, K. M., 1971b. Daily and seasonal man-biting activity of phlebotomine sandflies in Panamá. *J. Med. Entomol. 8:* 415-420.

CHRISTENSEN, H. A.; HERRER, A. & TELFORD, S. R. Jr. 1972. Enzootic cutaneous leishmaniasis in eastern Panamá. II. Entomological investigations. *Ann. trop. Med. Parasit. 66:* 55-66.

FAIRCHILD, G. B. & HERTIG, M. 1948. Notes on the *Phlebotomus* of Panama (Diptera: Psychodidae). III. *P. cruciatus* Coq., *trinidadensis* Newst. and *gomezi* Nitz. *Ann. ent. Soc. Am. 41:* 455-467.

FAIRCHILD, G. B. & THEODOR, O. 1971. On *Lutzomya flaviscutellata* (Mangabeira) and *L. ol-*

meca (Vargas and Diaz-Najera) (Diptera: Psychodidae). *J. Med. Entomol. 8:* 153-159.

FELICIANGELI, M. D. 1987. Ecology of sandflies (Diptera: Psychodidae) in a restricted focus of cutaneous leishmaniasis in Northern Venezuela. I. Description of the study area, catching methods and species composition. *Mem. Inst. Oswaldo Cruz*, 82 (1): 119-124.

FORATTINI, O. P. 1973. Entomologia Medica. IV. Psychodidae. Phlebotominae Leishmanioses. Bartonelose. Edgard Blucher, S. Paulo. 658 p.

FRAIHA, H.; SHAW, J. J. & LAINSON, R. 1971. Phlebotominae Brasileiros. II. *Psychodopygus wellcomei*, nova espécie antropófila de flebótomos do grupo *squamiventris*, do sul do Estado do Pará, Brasil (Diptera: Psuchodidae). *Mem. Inst. Oswaldo Cruz 69:* 489-500.

HANSON, W. J. 1961. The breeding places of *Phlebotomus* in Panama (Diptera: Psychodidae). *Rev. Bras. Biol. 29:* 383-389.

JOHNSON, P. T. & HERTIG, M. 1961. The rearing of *Phlebotomus* sandflies (Diptera: Psychodidae). II. Development and behaviour of Panamanian sandflies in laboratory culture. *Ann. ent. Soc. Amer. 54:* 764-776.

MARTINS, A. V.; WILLIAMS, P. & FALCAO, A. L. 1978. American Sandflies (Diptera: Psychodidae: Phlebotominae). *Acad. Brasil. Ciencias Río de Janeiro*, RJ. 195 p.

MILES, C. T.; FOSTER, W. A. & CHRISTENSEN, A. 1976. Mating aggregations of male *Lutzomya* sandflies at human hosts in Panama. *Trans. R. Soc. trop. Med. Hyg. 70:* 531-532.

MOGOLLON, J.; MANZANILLA, P. & SCORZA, J. V. 1977. Distribución altitudinal de nueve especies de *Lutzomya* (Diptera: Psychodidae) en el Estado Trujillo, Venezuela. *Bol. Dir. Malariol. y San. Amb. 17:* 206-229.

ORTIZ, I. 1968. Los flebótomos de venezuela en relación a la epidemiología de la Leishmaniasis Tegumentaria en el país. *Dermat. Venez. 7:* 530-538.

OSORNO MESA, E.; MORALES ALARCON, A.; de OSORNO, F. & FERRO-VELA, C. 1972. Phlebotominae de Colombia (Diptera: Psychodidae) IX. Distribución geográfica de especies de *Brumptomya* Franca & Parrot, 1921 y *Lutzomya* Franca, 1924 encontradas en Colombia, S. A. *Rev. Acad. colomb. Cienc. exact. fis. nat. 14:* 5-81.

PORTER, C. B. & De FOLIART, G.R., 1981. The manbiting activity of phlebotomine sandflies (Diptera: Psychodidae) in a tropical wet forest environment in Colombia. *Arq. Zool. S. Paulo, 30: 81-158.*

RUTLEDGE, L. C. & ELLENWOOD, D. A. 1975a. Production of Phlebotomine sandflies on the open forest floor in Panama. The species complement. *Environ. Entomol. 4:* 71-77.

RUTLEDGE, L. C. & ELLENWOOD, D. A. 1975b. Production of Phlebotomine sandflies on the open forest floor in Panama. Hydrologic and physiogeographic relations. *Environ. Entomol. 3:* 78-82.

RUTLEDGE, L. C. & ELLENWOOD, D. A. 1975c. Production of Phlebotomine sandflies on the open forest floor in Panama: Phytologic and edaphic relations. *Environ. Entomol. 4:* 83-89.

RUTLEDGE, L. C.; WALTON, B. C.; ELLENWOOD, D. A. & CORREA, M. A. 1976. A transect study of sandfly populations in Panama (Diptera: Psychodidae). *Environm. Entomol. 5:* 1149-1154.

SCORZA, J. V.; MOGOLLON, J. & MANZANILLA, P. 1979. Notas etológicas sobre *Lutzomya trinidadensis* (Newstead) (Diptera: Psychodidae) de Venezuela. *Bol. Dir. Malariol. y San. Amb. 19:* 35-38.

SHAW, J. J.; LAINSON, R. & WARD, R.D. 1972. Leishmaniasis in Brazil. VII. Further observations on the feeding habits of *Lutzomya flaviscutellata* (Mangabeira) with particular reference to its biting habits at different heights. *Trans. Roy. Soc. trop. Med. Hyg. 66:* 718-723.

THATCHER, V. E. & HERTIG, M. 1966. Field studies on the feeding habits and diurnal shelters of some *Phlebotomus* sandflies (Diptera: Psychodidae) in Panama. *Ann. entomol. Soc. Am. 59:* 46-52.

TESH, R. B.; CHANIOTIS, B. N.; ARONSON, M. D. & JOHNSON, K. M. 1971. Natural host preference of Panamanian Phlebotomine sandflies as determined by precipitin test. *Amer. J. trop. Med. Hyg. 20:* 150-156.

WARD, R. D.; SHAW, J. J.; LAINSON, R. & FRAIHA, H. 1973. Leishmaniasis in Brazil: VIII. Observations on the phlebotomine fauna of an area higly endemic of cutaneous leishmaniasis in the Serra dos Carajás, Pará State. *Trans. R. Soc. trop. Med. Hyg. 67:* 174-183.

WARD, R. D.; SHAW, J. J. & LAINSON, R. 1977. Hourly activity of *Lutzomyia flaviscutellata* (Diptera: Psychodidae), a vector of *Leishmania mexicana amazonensis.* Med. Ent. Centenary: Symposium Proceeding, London, *R. Soc. trop. Med. Hyg.:* 134-135.

WILLIAMS, P. 1970. Phlebotomine sandflies and Leishmaniasis in British Honduras (Belize). *Trans. R. Soc. trop. Med. Hyg. 64:* 317-318.

YOUNG, D. G., 1979. A review of the bloodsucking psychodid flies of Colombia (Diptera: Phlebotominae and Sycoracinae). *Univ. Fla. Exp. Stn. Tech. Bull. 806.* 266p.

ZELEDON, R.; MACAYA, G.; PONCE, C.; CHAVES, F.; MURILLO, J. & BONILLA, J. 1982. Cutaneous Leishmaniasis in Honduras, Central America. *Trans. R. Soc. trop. Med. Hyg. 76:* 276.