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PANAMANIAN *LUTZOMYIA* (DIPTERA: PSYCHODIDAE) HOST ATTRACTION PROFILES[1]

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Abstract. A study was carried out for 50 weeks in a tropical forest near the Pacific Ocean entrance to the Panama Canal to observe the host preferences of Phlebotomine sand flies. Ten mineral oil traps were baited with caged animals in the groups Marsupialia, Chiroptera, Primates, Edentata, Rodentia, Carnivora, Aves, Reptilia, and Amphibia, and included 1 empty control cage. *Lutzomyia vespertilionis* showed a distinct preference for bats. The host selections of *Lu. panamensis, Lu. olmeca bicolor* and *Lu. sanguinaria* were not as distinctive as those of *Lu. vespertilionis,* but mammals of the order Rodentia attracted the greatest number of these species. Host selections by the 4 sand fly species are discussed in relation to transmission of *Leishmania* and *Trypanosoma* species. A substantial number of females of the 12 most common sand fly species collected in animal-baited traps were gravid, suggesting a need for a blood meal prior to oviposition. CDC light trap collections, used in conjunction with the animal-baited traps, provided sufficient data to plot the seasonal densities of the 10 most common sand fly species at the study site.

The attractiveness of various sylvatic and domestic animals to Panamanian sand flies has been reported by Tesh et al. (1971, 1972) and Christensen & Herrer (1973). The general conclusions of these workers were that a few sand flies appeared to show distinct preferences, whereas the majority demonstrated variability in their host selection in different geographic areas. This variability was due, largely, to host availability and demonstrated that most *Lutzomyia* species studied were opportunistic feeders.

A study designed to afford *Lutzomyia* species equal accessibility to amphibians, reptiles, birds and 6 orders of mammals was conducted in a mature secondary forest area in central Panama over a period of 50 consecutive weeks (Oct. 1973–Sept. 1974). The purpose of the study was to eliminate the parameter of host availability in order to quantify host selection and thus determine host preferences.

MATERIALS AND METHODS

Study site

A study site 6.4 km west of Panama City was selected in the Rodman Ammunition Depot on the Pacific slope of Panama in the former Canal Zone. The climate is seasonal, with a dry season extending from mid-December to mid-April. The forest is composed of second-growth shrubs and trees that grow to 18 m in height with associated vines and epiphytes, and has been classified as Dry Tropical Forest (Holdridge & Budowski 1956, Holdridge 1967).

The specific site was selected at the end of a small valley near a creek in which there was a continuous flow of water throughout the year.

Experimental design

Ten animal cages, each 61 × 61 × 122 cm, were arranged in 2 parallel rows back to back 30.5 cm above the forest floor (Fig. 1). The cages were wooden framed and enclosed by 1.5-cm wire mesh screen with an access door at the top. The back, sides and top of each cage were covered with burlap. Four shallow metal traps, 30.5 × 46 cm, were placed on the ground in front of each cage and coated with mineral oil to trap approaching sand flies. A corrugated metal roof protected the animals and oil traps from the frequent rains during the wet season. Categories of animals used as bait in each cage were assigned letters as follows: A, edentate; B, rodent; C, marsupial; D, primate; E, carnivore; F, chiropteran; G, bird; H, reptile; I, amphibian; and J, control (empty cage). The oil pan traps fronting each cage were assigned numbers from 1–10. The cages with their animals were randomly assigned weekly to the 10 traps. The Latin Square randomization design assured that during a 10-week period each category of animal (including control) occurred once and only once at each oil trap. Different animal species within each category were changed only at the beginning of each 10-week period. The traps, which were inspected on a daily basis for 50 weeks, were removed for 24 h every week and 2 CDC miniature light traps operated from 1800 h to 0600 h during this period.

RESULTS

A total of 3525 sand flies of 21 species were collected in the CDC light traps (Table 1). Three species, *Lu. vespertilionis, Lu. carpenteri* and *Lu. pan-*

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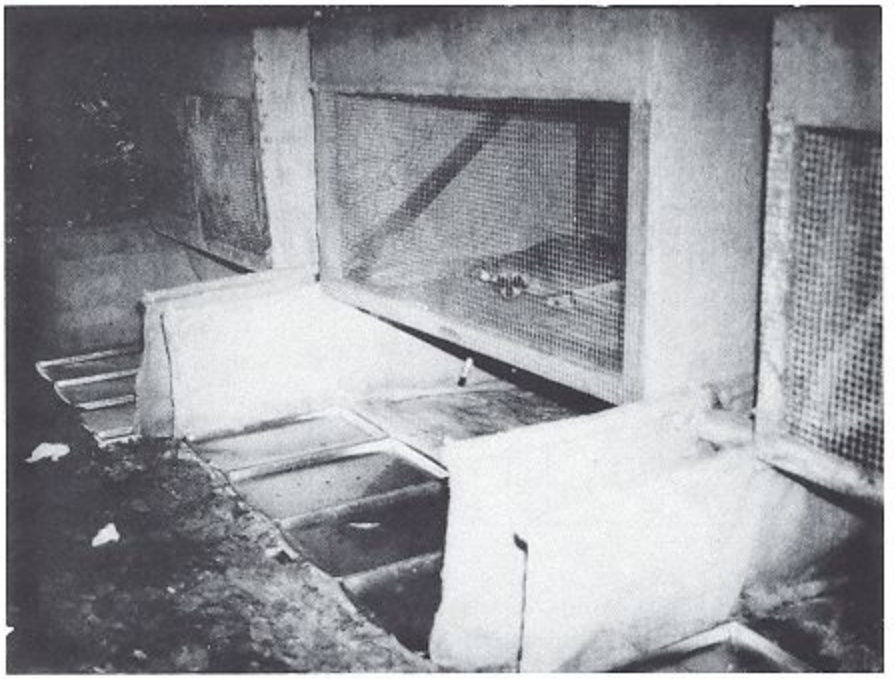

FIG. 1. Three of 10 mineral oil traps with caged bait animals at study site. Animal in center cage: Raccoon, *Procyon cancrivorus* (Carnivora: Procyonidae).

amensis, accounted for 74% of the total flies collected by this method. Sex ratios of males to females ranged from a high of 1.5:1 for *Lu. sanguinaria* to a low of 0.2:1 for *Lu. panamensis* and *Lu. trapidoi*. Over ½ of the females of *Lu. gomezi* and *Lu. trapidoi* attracted to the light traps were gravid. A lesser percentage of all other species taken also were gravid.

A total of 2640 sand flies of 22 species were collected from the animal-baited oil traps (TABLE 2). Three species, *Lu. vespertilionis, Lu. panamensis* and *Lu. olmeca bicolor*, accounted for 86% of the total flies collected in these traps. *Lu. carpenteri* represents the only species in which the number of males exceeded the number of females in the baited traps. *Lu. olmeca bicolor, Lu. trapidoi* and *Lu. gomezi* showed the lowest male to female ratio in these collections. The majority of females of *Lu. ovallesi, Lu. trapidoi* and *Lu. gomezi* were gravid at the time they approached the animals. As in the case of light trap collections, a lesser percentage of all other species collected also showed egg maturation.

Comparisons among the 12 most common

TABLE 1. Abundance, sex ratio and gravidity among phlebotomine sand flies collected by CDC light traps, October 1973–September 1974.

Lutzomyia SPECIES	NO.	% OF TOTAL	SEX RATIO ♂ : ♀	% ♀ GRAVID
vespertilionis	1347	38.2	0.9:1	2.1
carpenteri	853	24.2	1.1:1	11.6
panamensis	398	11.3	0.2:1	12.5
trapidoi	158	4.5	0.2:1	68.7
ovallesi	155	4.4	0.5:1	45.3
olmeca bicolor	141	4.0	0.3:1	29.9
camposi	130	3.7	0.8:1	2.8
pessoana	103	2.9	0.4:1	20.8
sanguinaria	69	2.0	1.5:1	17.9
gomezi	63	1.8	0.4:1	76.1
dysponeta	43	1.2	0.5:1	3.6
10 additional spp.	65	1.8		

TABLE 2. Abundance, sex ratio and gravidity among phlebotomine sand flies collected by animal-baited oil traps, October 1973–September 1974.

Lutzomyia SPECIES	NO.	% OF TOTAL	SEX RATIO ♂ : ♀	% ♀ GRAVID
vespertilionis	1538	58.3	0.8:1	8.8
panamensis	382	14.5	0.5:1	6.2
olmeca bicolor	341	12.9	0.1:1	20.7
sanguinaria	92	3.5	0.3:1	3.2
trinidadensis	46	1.7	0.4:1	3.0
trapidoi	37	1.4	0.1:1	71.4
ovallesi	33	1.3	0.3:1	80.8
carpenteri	28	1.1	1.2:1	46.2
dysponeta	28	1.1	0.5:1	21.1
camposi	26	1.0	0.4:1	36.8
pessoana	18	0.7	0.2:1	26.7
gomezi	13	0.5	0.1:1	50.0
10 additional spp.	58	2.2		

TABLE 3. Relative phototropism among 12 common phlebotomine sand fly species, October 1973–September 1974.

Lutzomyia species	No. sand flies: Light trap (LT)	No. sand flies: Animal bait (AB)	Ratio LT:AB
carpenteri	853	28	30.5:1
pessoana	103	18	5.9:1
camposi	130	26	5.0:1
gomezi	63	13	4.8:1
ovallesi	155	33	4.7:1
trapidoi	158	37	4.3:1
dysponeta	43	28	1.5:1
panamensis	398	382	1.0:1
vespertilionis	1347	1538	0.9:1
sanguinaria	69	92	0.7:1
olmeca bicolor	141	341	0.4:1
trinidadensis	16	46	0.3:1

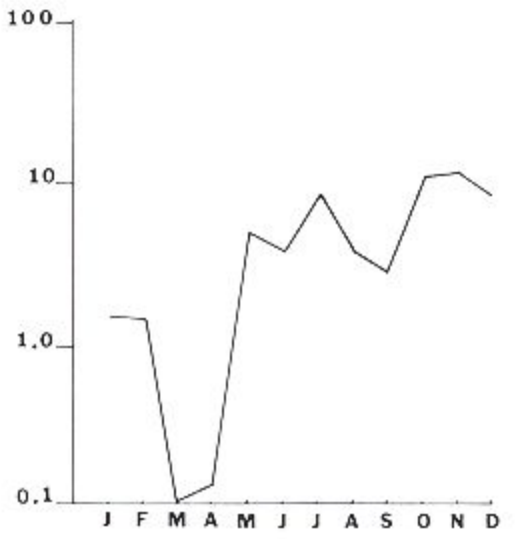

FIG. 2. Annual rainfall in inches reported by the Panama Canal Company Meteorological and Hydrographic Branch from a recording station 4.8 km east of the study site during the period of investigation.

species, in relation to their numbers in light traps versus animal-baited traps, provided an indication of their relative phototrophism (TABLE 3). *Lu. carpenteri*, whose feeding habits are virtually unknown, showed a prevalence in light traps versus animal-baited traps 5 times greater than *Lu. pessoana*, the second most photophilic species. *Lu. trinidadensis*, one of the most common species found in tree buttresses in Panama, showed the least relative attraction to light.

Rainfall (FIG. 2) appears to be the most important determinant of seasonal densities among many species of sand flies, although the lack of correlation with the prevalence of certain species (FIG. 3) demonstrates that other abiotic and biotic factors are involved. Populations of *Lu. vespertilionis, Lu. panamensis, Lu. olmeca bicolor, Lu. camposi* and *Lu. pessoana* were highest during the wet season, whereas the greatest densities of *Lu. trapidoi, Lu. ovallesi, Lu. sanguinaria* and *Lu. gomezi* occurred during the dry season. The erratic fluctuation in the abundance of *Lu. carpenteri* appeared unrelated to rainfall.

Collections of the 4 commonest sand flies in the animal-baited traps, *Lu. vespertilionis, Lu. panamensis, Lu. olmeca bicolor* and *Lu. sanguinaria*, are detailed in TABLE 4 to show their relative abundance in the traps of all bait-animal species used in the study. The paucity of blood-engorged phlebotomines may be attributed to the efficacy of the mineral oil pans in trapping the flies as they approached the animals. The absence of blood-engorged specimens in the control trap attests to the insular effect of each trap system and the high probability that the engorged flies in animal-baited traps had indeed fed on the caged animal associated with each trap.

A chi-square goodness of fit test for the hypothesis of equal host preference was performed for *Lu. vespertilionis, Lu. olmeca bicolor, Lu. panamensis* and *Lu. sanguinaria*, which showed a rejection in each case at the 0.01 level, indicating significant host preferences for these species.

With the exception of *Lu. vespertilionis*, which showed a definite preference for bats, the other 3 species exhibited a discernible preference for rodents (FIG. 4).

Amphibia were clearly the least attractive of the 4 animal classes studied and, with the exception of *Lu. sanguinaria*, accounted for less flies than the empty control cage, which may indicate a definite aversion.

Reptiles appeared almost as unattractive as amphibians, whereas birds were second to mammals in their attractiveness to the 4 commonest sand fly species.

DISCUSSION

Phlebotomine sand flies are primitive nematoceran Diptera with weak flight ability and short-range dispersal. Their short hoplike flights over the forest floor and tree branch pathways increase their opportunity of encountering hosts. Such flight habits would be advantageous to any primitive hematophagous arthropod with poorly developed host detection systems. However, the distinct

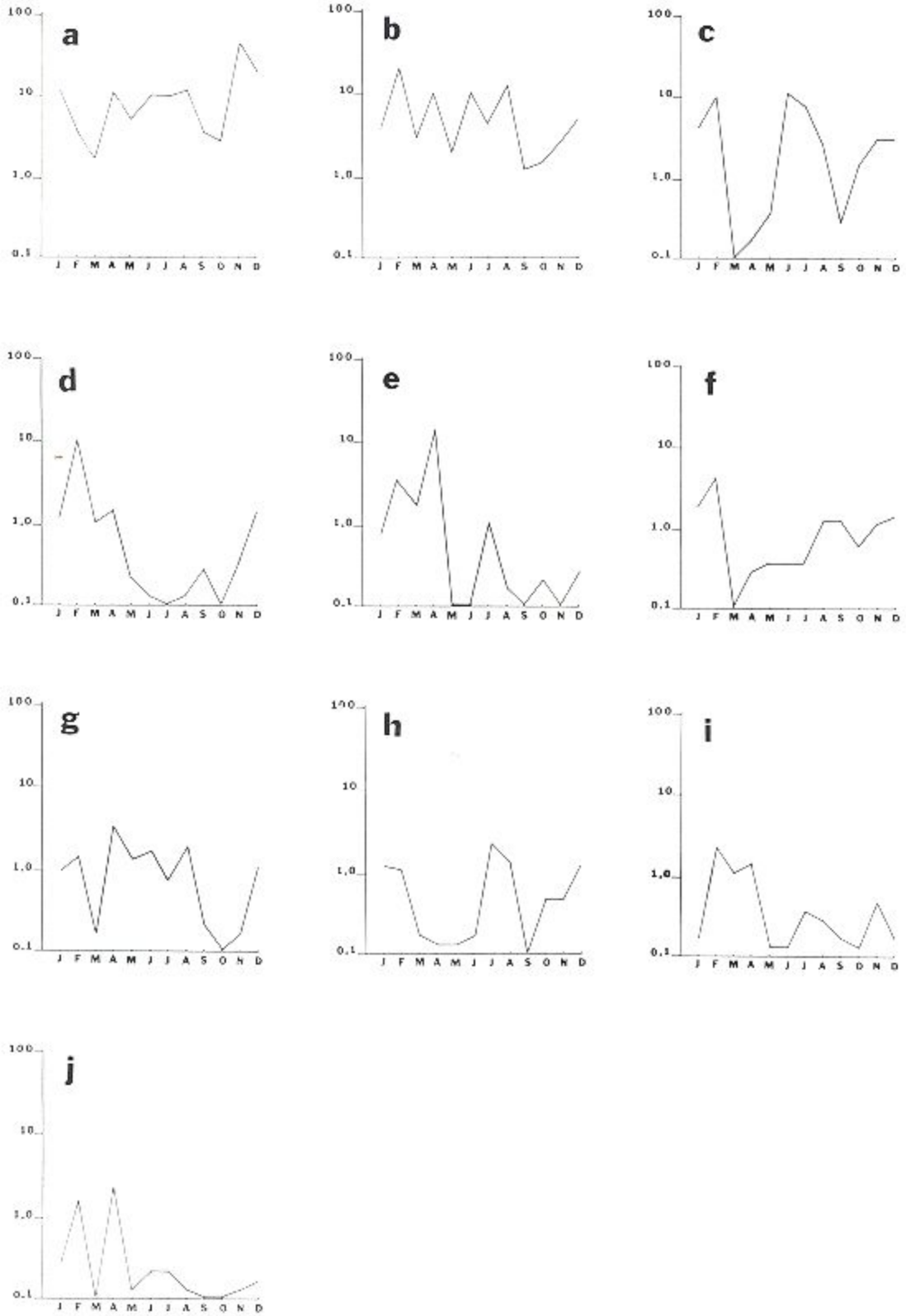

FIG. 3. a–j. Seasonal densities of the 10 most common sand fly species as recorded from light trap collections (mean number of each species per trap-night per month): a, *Lu. vespertilionis*; b, *Lu. carpenteri*; c, *Lu. panamensis*; d, *Lu. trapidoi*; e, *Lu. ovallesi*; f, *Lu. olmeca bicolor*; g, *Lu. camposi*; h, *Lu. pessoana*; i, *Lu. sanguinaria*; j. *Lu. gomezi*.

TABLE 4. Animal-baited oil trap collections of ♀ of the 4 most common phlebotomine sand flies, October 1973–September 1974.

BAIT-ANIMAL SPECIES	NO. WEEKS EXPOSURE	*Lutzomyia* SPECIES			
		vespertilionis No. ♀/No. engorged	*o. bicolor* No. ♀/No. engorged	*panamensis* No. ♀/No. engorged	*sanguinaria* No. ♀/No. engorged
Marsupialia					
Didelphis marsupialis	40	32/3	29/1	16/4	3/1
Caluromys derbianus	10	16/0	7/0	6/0	0/0
Chiroptera					
Carollia perspicillata	50	364/103	23/0	14/2	1/0
Primates					
Cebus capucinus	20	6/1	21/0	9/2	2/0
Ateles fusciceps	10	2/0	5/0	7/1	8/5
Saguinus geoffroyi	20	22/0	8/0	7/0	0/0
Edentata					
Bradypus infuscatus	10	21/3	0/0	3/0	0/0
Choloepus hoffmanni	40	45/1	24/1	12/1	4/0
Rodentia					
Sigmodon hispidus	10	7/0	45/1	6/0	1/0
Coendou rothschildi	10	15/0	12/0	54/2	13/1
Dasyprocta punctata	20	28/0	9/0	10/0	4/0
Proechimys semispinosus	10	4/0	4/1	2/0	0/0
Carnivora					
Canis familiaris	10	6/1	5/0	27/4	3/1
Procyon cancrivorus	20	51/0	16/0	12/0	3/1
Potos flavus	10	6/0	3/0	10/0	2/0
Felis catus	10	1/0	23/3	3/1	2/0
Aves					
Chicken and pigeon	10	3/0	4/0	13/1	4/4
Ortalis cinereiceps	10	6/0	10/1	7/1	2/0
Columba livia	10	0/0	12/1	3/0	0/0
Aratinga pertinax	10	16/1	2/0	3/0	1/0
Thraupis episcopus	10	24/0	2/0	1/0	3/0
Reptilia					
Kinosternon leucostotum and *Iguana iguana*	10	4/0	1/0	3/1	0/0
Geomyda annulata	20	21/0	11/0	9/0	1/0
Thecadactylus rapicauda	2	0/0	3/0	1/0	0/0
Boa constrictor	18	20/0	11/1	7/0	1/0
Amphibia					
Leptodactylus pentadactylus	30	0/0	0/0	0/0	0/0
Bufo marinus	20	11/1	18/1	6/1	1/1
Control	50	50/0	25/0	11/0	1/0

preference for bats by *Lu. vespertilionis* and the clearly evident selection of mammals, especially rodents, by *Lu. panamensis, Lu. olmeca bicolor* and *Lu. sanguinaria,* collected in numbers substantially greater than those from the empty control cage, indicate that these species are able to detect acceptable hosts at a distance of greater than 1 m (distance of forest floor fronting oil collecting trays to rear of cages 1.5 m).

A significant percentage of female sand flies attracted to light and to animals were gravid. This rate would be substantially greater if recently emerged nulliparous females had been excluded. Blood engorgement shortly preceding oviposition may provide a survival mechanism, since the fresh blood meal could provide an immediate source of fluids and energy, to be expended during egg-laying, and therefore ameliorate the trauma associated with oviposition. The observation of this behavioral sequence of events in nature may demonstrate an important consideration previously overlooked in attempts to colonize New

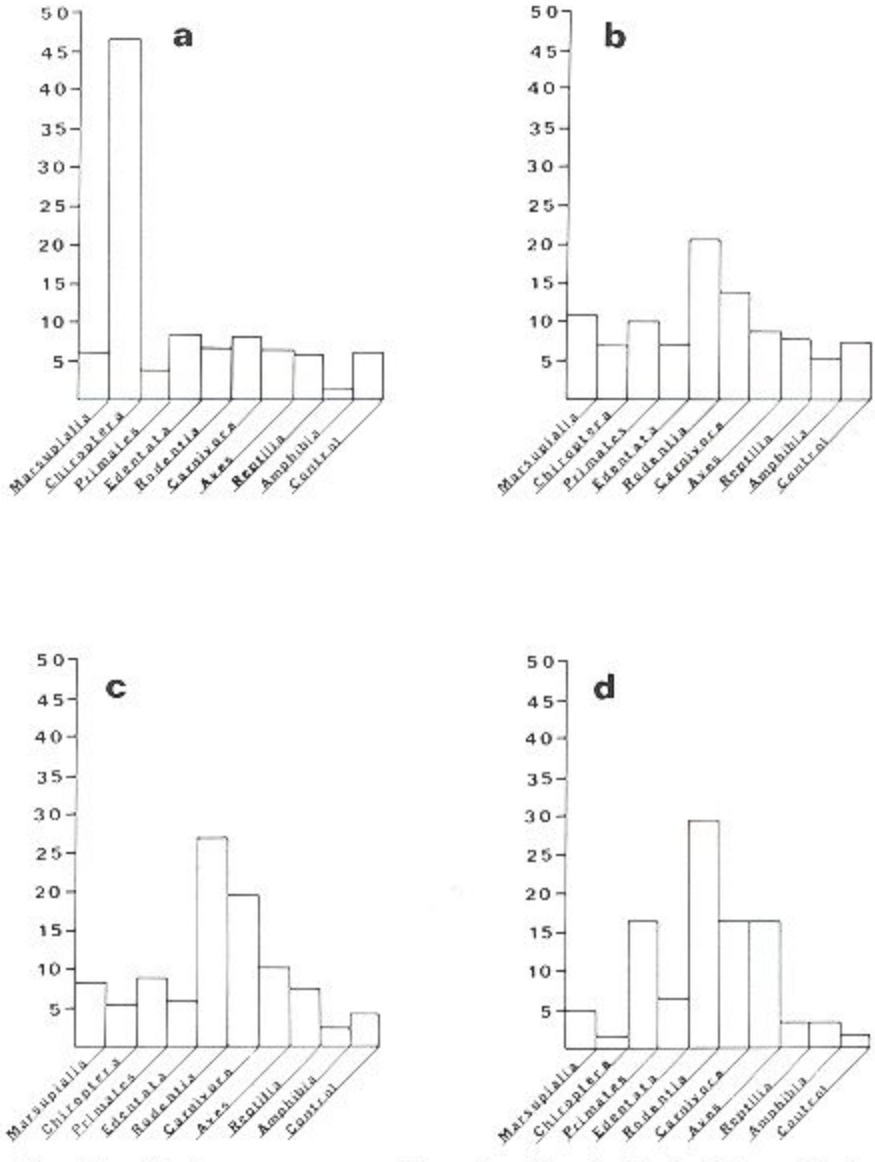

FIG. 4. a–d. Densities of the 4 most common sand flies collected in animal-baited oil traps (% of total collected from each animal-baited trap); a, *Lu. vespertilionis*; b, *Lu. panamensis*; c, *Lu. olmeca bicolor*; d, *Lu. sanguinaria*.

World sand flies, since the highest rate of mortality has occurred during or shortly following oviposition in our former colonies of *Lu. sanguinaria* and *Lu. gomezi* (Christensen, unpubl. information).

Animal size did not appear to be a critical factor in host selection since the rodents and bats used in the study were the smallest species of mammals, yet attracted the majority of flies.

It was not surprising to find the greatest number of *Lu. olmeca bicolor* in traps baited with rodents. This species has been implicated as the vector of Panamanian *Leishmania mexicana*, whose principal reservoirs are rodents (Christensen et al. 1972; Herrer et al. 1971).

Lu. panamensis and *Lu. sanguinaria* have been implicated as vectors of *Le. braziliensis* in Panama (Christensen & Herrer 1973). Although *Le. braziliensis* was isolated from 10.5% of 200 Spiny Rats, *Proechimys semispinosus*, in 1956 and 1957 (Hertig et al. 1958), the search for this parasite in 1504 rodents of 21 species since that time has been unsuccessful (Herrer et al. 1973). The fact that neither of these 2 vector species showed any detectable preference for the Two-toed Sloth, *Choloepus hoffmanni*, the principal reservoir host of *Le. braziliensis* in Panama (Herrer et al. 1973), was surprising. Our past experience has shown that the Two-toed Sloth is highly susceptible to *Le. brazil-*

iensis, which infects the viscera as well as the skin for long periods of time (Herrer & Christensen 1977). Persistent infections in sloths may help to explain the high prevalence of the disease in this animal despite the apparent low level of attractiveness for 2 vector species.

Lu. vespertilionis has been implicated as a vector of *Trypanosoma leonidasdeanei,* a parasite of the El Salvador Sheath-tailed Bat, *Saccopteryx bilineata,* in Costa Rica (Zeledón & Rosabal 1969) and in Panama (Christensen & Herrer 1975). Tesh et al. (1972) reported that 100% of 40 *Lu. vespertilionis* blood meals, tested by the precipitin method, were positive for bats. The present study, although corroborating the findings of the above workers, showed that occasionally this phlebotomine also will feed on marsupials, primates, edentates, carnivores, birds and amphibians. Evidence was presented also that *Eu. olmeca bicolor* and *Lu. panamensis* may rarely feed on birds, reptiles and amphibians. *Lu. sanguinaria* occasionally feeds on birds and amphibians.

The sand fly species studied have shown varying degrees of host preference, but all have been found to be opportunistic feeders.

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