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THE TREE-BUTTRESS BIOTOPE: A PATHOBIOCENOSE OF *LEISHMANIA BRAZILIENSIS**

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Abstract. A total of 52,033 sandflies, comprising 33 species, was collected in tree buttresses in Panama. Of the 18,025 females collected, 1,592 (8.8%) engorged phlebotomines of 18 species contained sufficient blood for identification of their vertebrate hosts by the microcapillary precipitin method. *Lutzomyia ylephiletor* and *Lu. trapidoi,* vectors of *Leishmania braziliensis,* had fed predominantly on sloths (47.0% and 65.1%, respectively). *Lutzomyia shannoni,* a common non-anthropophilic sandfly in tree buttresses also fed most frequently on sloths (28.0%) and probably also contributes to the *Leishmania* transmission cycle among the edentates. Two-toed sloths (*Choloepus hoffmanni*), the principal reservoir of *L. braziliensis* in Panama, cohabit the same arboreal bioptope with these sandfly species. *Leishmania braziliensis* was isolated in culture from 14 of 68 (20.6%) *C. hoffmanni* captured in the study sites during the period of this investigation. The data illustrate that the buttresses of large trees in Panama represent potential pathobiocenose bioptopes of *L. braziliensis.* Other sandfly species tested for host-feeding sources included: *Lu. trinidadensis,* which fed preferentially on reptiles; *Lu. triramula, Lu. ovallesi,* and *Lu. camposi* fed most frequently on armadillos. The hosts of 11 additional sandfly species were identified; however, the numbers recorded were too small to discern distinct feeding patterns among these phlebotomines.

Habitats of sylvatic neotropical sandflies include a diversity of biotopes such as forest floor litter, green plants, caves, animal burrows, tree hollows and tree buttresses. Tree buttresses represent a resting site which provides a stable microenvironment and optimal preferenda for sandflies throughout the diel period, and one in which large numbers and a diversity of phlebotomines congregate. Many of the large trees, such as *Ficus, Ceiba* and *Sterculia* spp., in the forests of Panama and other neotropical countries produce lateral extensions of the trunk base to form extensive buttresses. Four species of the indigenous sandfly fauna, *Lutzomyia ylephiletor, Lu. trapidoi, Lu. panamensis* and *Lu. gomezi,* which utilize this biotope, have been implicated as vectors in Panama of *Leishmania braziliensis.*[1–4] Many of the buttressed trees are also draped with vines that extend from the forest canopy to the ground. Two-toed sloths (*Choloepus hoffmanni*), the principal reservoir host of *L. braziliensis* in this country,[5,6] utilize the vines to migrate between the forest floor and the canopy (Figs. 1 and 2). Sloths usually rest during the day in forks and branches of large trees or clumps of tangled vines associated with such trees. Occasionally, at night, the animals descend the vines to the forest floor within the tree buttresses to defecate and urinate. Chaniotis et al.[7] reported that *Lu. ylephiletor* and *Lu. trapidoi,* the two most common vector species occurring on tree trunks, are more abundant in the vicinity of the base of large trees; however, they were collected up to 9 m and 15 m, respectively. Since the vectors and the principal reservoir host of *L. braziliensis* share the same biocenose, we were interested in determining if these sandflies were feeding on the sloths and, if so, the frequency of such feedings, since this relationship has relevance to the phlebotomine's involvement in the transmission of the parasite.

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MATERIALS AND METHODS

Study sites

The investigation was conducted in five study sites in Panama during the period from July 1979 to December 1980 (Fig. 3). Two known endemic areas of *L. braziliensis* were selected as the principal study sites for capturing sloths and collecting sandflies from tree buttresses, El Aguacate, Pan-

FIGURE 1. The two-toed sloth (*Choloepus hoffmanni*), principal reservoir host of *Leishmania braziliensis* in Panama.

ama Province, and Mojinga Forest, Fort Sherman Reservation, Colón Province. El Aguacate is a small rural agricultural community of approximately 200 people located in the foothills of Trinidad Mountain, about 45 km west of Panama City. Many of the large trees, left uncut to provide shade for the coffee plants, support dense populations of sandflies; sloths are relatively common in this area. In 1969, 42% of the people surveyed in this settlement had leishmanoid scars or active lesions,[8] and this hyperendemic condition has persisted until now. Mojinga is a lowland tropical rain forest within the Fort Sherman Army Reservation. This study site is approximately 5 km from the Caribbean coast, and is used for training military troops in the techniques of jungle warfare. The annual incidence of cutaneous leishmaniasis among soldiers participating in these operations from 1960 to 1976 ranged from 2 to 45 cases, and in 1977, 10 of 627 (1.6%) of the soldiers contracted the disease.[9]

The primary forest surrounding a hydroelectric engineering camp at Corriente Grande, Bocas del Toro Province was selected as a third study area endemic for *Leishmania* (Figs. 3 and 4). Sandflies were also collected in tree buttresses occasionally

FIGURE 2. *Choloepus hoffmanni* (arrow) attempting to escape from fieldmen by climbing a vine associated with a large, buttressed tree in the Mojinga Forest.

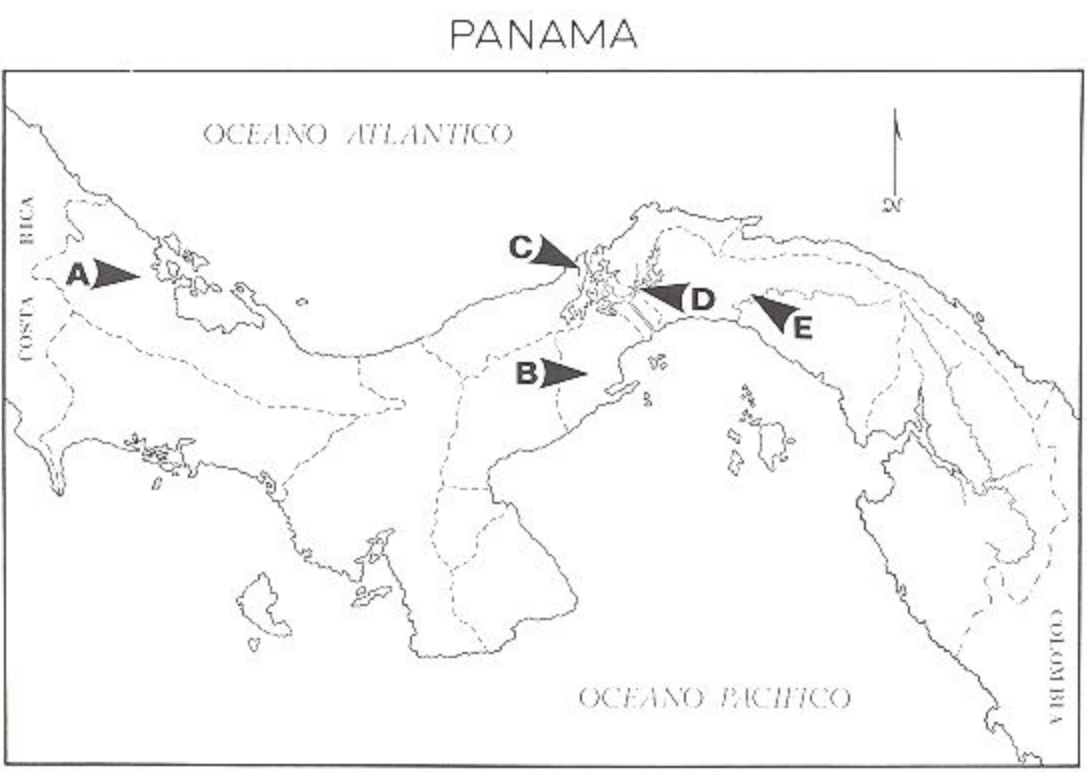

FIGURE 3. Study sites where sandflies were collected from tree buttresses for host determinations by the microcapillary precipitin test. (A) Corriente Grande, Bocas del Toro Province; (B) El Aguacate, Panama Province; (C) Mojinga Forest, Colón Province; (D) Juan Mina, Panama Province; (E) Maje, Panama Province.

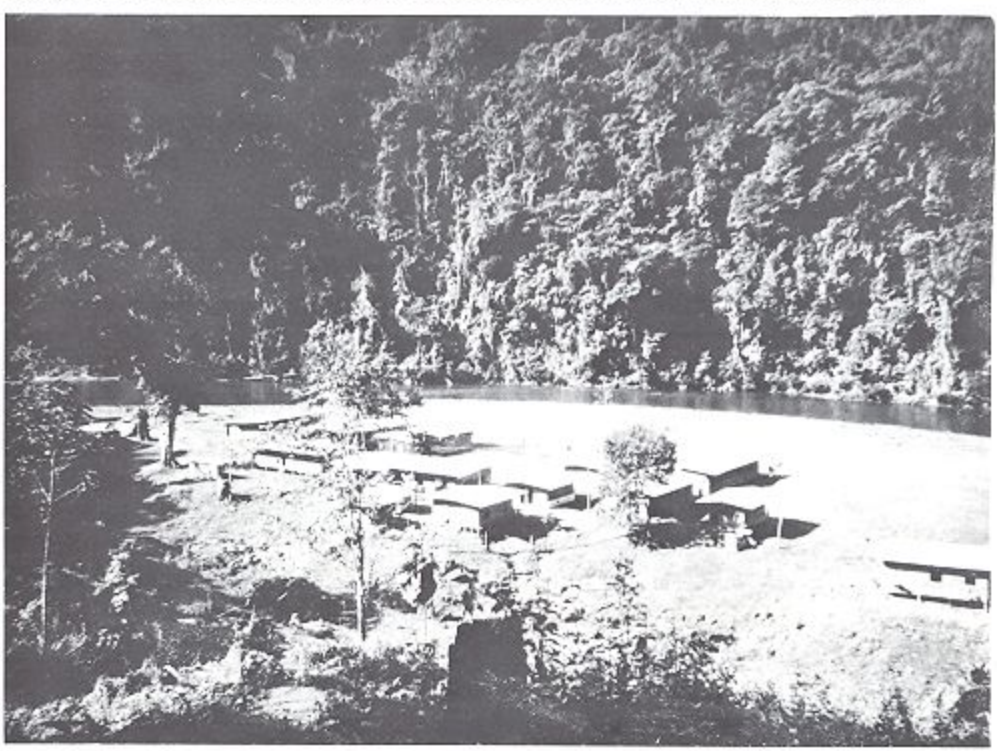

FIGURE 4. A hydroelectric engineering campsite by the Changuinola River at Corriente Grande, Bocas del Toro Province. This region is highly endemic for *Leishmania braziliensis*.

TABLE 1

Sandflies collected from tree buttresses in Panama July 1979 to December 1980

Sandfly spp.	Males	Females	Ratio	Total	%
*Lu. ylephiletor**	14,806	7,706	1.9:1	22,512	43.3
Lu. trinidadensis	10,463	6,795	1.5:1	17,258	33.2
Lu. shannoni	4,176	1,315	3.2:1	5,491	10.6
Lu. triramula	1,744	359	4.9:1	2,103	4.0
Lu. ovallesi	1,149	435	2.6:1	1,584	3.0
Lu. vespertilionis	969	89	10.9:1	1,058	2.0
*Lu. gomezi**	98	369	0.3:1	467	0.9
*Lu. panamensis**	22	337	0.1:1	359	0.7
*Lu. trapidoi**	149	186	0.8:1	335	0.6
Lu. camposi	111	177	0.6:1	288	0.6
Br. hamata	72	37	1.9:1	109	0.2
Lu. sanguinaria	14	64	0.2:1	78	0.1
Lu. lichyi	39	38	1.0:1	77	0.1
Lu. cruciata	32	29	1.1:1	61	0.1
19 other spp.†	164	89		253	0.5
Total	34,008	18,025		52,033	100

* Sandfly species incriminated as vectors of *Leishmania braziliensis* in Panama.

† *Lu. aclydifera, Lu. barretoi, Lu. olmeca bicolor, Lu. carpenteri, Lu. cayennensis, Lu. chassignetti, Lu. dasymera, Lu. disponeta, Lu. furcata, Br. galindoi, Lu. gorbitzi, Lu. micropyga, Lu. personata, Lu. punctigeniculata, Lu. runoides, Lu. sandesti, Lu. serrana, Lu. undulata, Lu. vexillifera*

from two additional forested study sites in Panama Province, Maje, and Juan Mina (Fig. 3).

Sandfly collections

Weekly and biweekly collections of phlebotomines from tree buttresses were made over the 18-month study period beginning in July 1979 in El Aguacate and Mojinga Forest, respectively. Sandflies were also collected periodically from tree buttresses in Corriente Grande over 10-day periods in December 1979 and January, February and March 1980. Mouth- and battery-operated aspirators were used to collect the phlebotomines, and all collections were then sent to Gorgas Memorial Laboratory (GML) for identification. Blood-engorged females were stored at −5°C prior to blood-meal source determinations.

Blood meal analysis

The microcapillary precipitin test was used to identify the vertebrate host source for the blood-engorged flies. The methods used in the preparation of antisera and performance of the test have been detailed previously.[10]

Sloth capture

Two-toed sloths were captured by hand from trees in El Aguacate and Mojinga Forest and brought to GML for detection of leishmanial infections. The tissue-biopsy-culture technique[11] was used for isolation of *Leishmania* in Senekjie's blood agar medium. Identification of promastigotes cultured was determined by their infectivity and pathogenesis to golden hamsters, *Mesocricetus auratus,* and by isozyme profiles, using cellulose acetate membrane electrophoresis,[12] for the following enzymes: acid phosphatase, alanine amino-transferase, aspartate amino-transferase, glucose 6-phosphate dehydrogenase, phosphoglucoisomerase and fructokinase.

RESULTS

Sandfly fauna in tree buttresses

A total of 52,033 sandflies comprising 33 species was collected from tree buttresses in the five study sites. Table 1 illustrates the diversity and density of phlebotomine species in the tree-buttress biotope. Although the relative numbers of certain species differed slightly in each area, *Lu. ylephiletor* was the predominant sandfly in all of the study sites. Of the 18,025 females collected 1,592 (8.8%) engorged phlebotomines of 18 species contained sufficient blood for identification of their vertebrate hosts.

Sandfly blood meal analysis

The vertebrate hosts of 1,017 *Lu. ylephiletor* females collected from tree buttresses were iden-

tified (Table 2). Animals from 26 families representing mammals, birds, reptiles and amphibians were fed on by this *Leishmania* vector; 97% of the blood meals were derived from mammals. Sloths were the principal source of blood, comprising almost half (47.0%) of the blood meals. Porcupines and anteaters were the second and third most frequent hosts of *Lu. ylephiletor* (9.7% and 7.1%, respectively). Feedings on vertebrates of two families, Myrmecophagidae and Dasypodidae, were detected in one female. Genera-specific antisera against the two indigenous sloth species, *C. hoffmanni* and *Bradypus infuscatus*, were developed late in the study and tested against 47 of the 478 *Lu. ylephiletor* which had fed on Bradypodidae; all were positive for *Choloepus* and negative for *Bradypus*.

Lutzomyia trapidoi, another *Leishmania* vector species, fed exclusively on mammals and predominantly on sloths (65.1%) (Table 2).

Blood-engorged *Lu. gomezi* and *Lu. panamensis* females, also vectors of *Leishmania*, were not collected in sufficient numbers to determine specific feeding patterns (Table 2), although half of the latter species had fed on perissodactyls (probably horses). A double feeding on a chicken and an unidentified mammal was also detected in one *Lu. panamensis*.

Lutzomyia shannoni (Table 3) fed most frequently on sloths (28.0%) followed by anteaters (13.1%) and porcupines (11.3%); 5 of 47 blood meals positive for Bradypodidae and tested at the generic level were positive for *C. hoffmanni*.

Lutzomyia trinidadensis was the second most common sandfly collected from tree buttresses. This species was found to feed preferentially on reptiles (61.3% of all feedings) and particularly on lizards (Table 3).

Armadillos were the predominant hosts for *Lu. triramula* and comprised over three-fourths (76.0%) of its blood meals (Table 3).

The vertebrate hosts for *Lu. ovallesi* were primarily members of the order Edentata which accounted for 55.8% of its feedings (Table 3); armadillos and sloths were the principal hosts of this species (21.2% and 17.3%, respectively). Reptilians were also fed on by *Lu. ovallesi* (15.3%).

The vertebrate hosts of 10 additional sandfly species were identified as follows:

Lutzomyia camposi (32 host identifications): 12 (37.5%) armadillos; 7 (21.9%) rabbits; 6 (18.8%) unidentified mammals; 4 (12.5%) unidentified edentates; 3 (9.4%) anteaters.

Lutzomyia vespertilionis (9 host identifications): 4 bats, and 1 each opossum, porcupine, rabbit, lizard and unidentified edentate.

Brumptomyia hamata (6 host identifications): 3 rabbits and 3 armadillos.

Lutzomyia sanguinaria (5 host identifications): 1 each man, unidentified primate, rabbit, porcupine and unidentified mammal.

Lutzomyia saulensis (4 host identifications): 1 armadillo and 3 unidentified mammals.

Lutzomyia serrana, Lu. carpenteri, Lu. barretoi, Lu. lichyi, and *Lu. olmeca bicolor* (1 host identification each): a leaf-nosed bat, an armadil-

TABLE 2

Vertebrate hosts, determined by microcapillary precipitin tests, of four Leishmania *vector sandfly species collected from tree buttresses in Panama*

	Lutzomyia spp.							
	ylephiletor		*trapidoi*		*gomezi*		*panamensis*	
Vertebrate host	No.	(%)	No.	(%)	No.	(%)	No.	(%)
MAMMALIA								
Unidentified	72	(7.1)	5	(11.6)	6	(20.0)	1	(3.8)
Marsupialia								
Didelphidae (opossums)	21	(2.1)	1	(2.3)	2	(6.7)		
Chiroptera								
Unidentified	1	(0.1)						
Phyllostomatidae (leaf-nosed bats)	1	(0.1)						
Primates								
Unidentified	14	(1.4)			7	(23.3)	1	(3.8)
Hominidae (man)	15	(1.5)	2	(4.7)				
Cebidae (monkeys)	3	(0.3)	2	(4.7)				
Callithricidae (marmosets)					4	(13.3)		

TABLE 2
Continued

Vertebrate host	*Lutzomyia* spp.							
	yuilli		*trapidoi*		*gomezi*		*panamensis*	
	No.	(%)	No.	(%)	No.	(%)	No.	(%)
Edentata								
Unidentified	39	(3.8)	1	(2.3)				
Bradypodidae (sloths)	478	(47.0)	28	(65.1)	2	(6.7)	1	(3.8)
Myrmecophagidae (anteaters)	72	(7.1)	1	(2.3)	1	(3.3)		
Dasypodidae (armadillos)	4	(0.4)	1	(2.3)	1	(3.3)		
Lagomorpha								
Leporidae (rabbits)	45	(4.4)	1	(2.3)	4	(13.3)	4	(15.4)
Rodentia								
Unidentified	4	(0.4)						
Erethizontidae (porcupines)	99	(9.7)					2	(7.7)
Cricetidae (rice rats)	1	(0.1)						
Sciuridae (squirrels)	3	(0.3)						
Echimyidae (spiny rats)	1	(0.1)						
Carnivora								
Unidentified					1	(3.3)		
Musterlidae (weasels, skunks)	1	(0.1)						
Canidae (dogs, foxes)	1	(0.1)						
Procyonidae (raccoons, coatis)	3	(0.3)						
Perissodactyla								
Unidentified (horses, tapirs)	55	(5.4)	1	(2.3)	1	(3.3)	13	(50.0)
Artiodactyla								
Unidentified	1	(0.1)						
Bovidae (cows)	44	(4.3)						
Suidae (pigs)	1	(0.1)			1	(3.3)	1	(3.8)
Cervidae (deer)	8	(0.8)					1	(3.8)
			AVES					
Unidentified	4	(0.4)						
Anseriformes								
Anatidae (ducks)							1	(3.8)
Caprimulgiformes								
Nyctibiidae (potoo)							1	(3.8)
Galliformes								
Cracidae (curassows, guans)	1	(0.1)						
Ciconiiformes								
Ardeidae (herons)	1	(0.1)						
Cuculiformes								
Cuculidae (cuckoos, anis)	1	(0.1)						
Passeriformes								
Thraupidae (tanagers)	1	(0.1)						
			REPTILIA					
Unidentified	4	(0.4)						
Sauria (lizards)	14	(1.4)						
Serpentilia (snakes)	1	(0.1)						
			AMPHIBIA					
Unidentified	3	(0.3)						
Total blood meals identified	1,017	(100)	43	(100)	30	(100)	26	(100)

TABLE 3

Vertebrate hosts, determined by microcapillary precipitin tests, of four common sandfly species collected from tree buttresses in Panama

Vertebrate host	*Lutzomyia* spp.							
	shannoni		*trinidadensis*		*triramula*		*pilosa*	
	No.	(%)	No.	(%)	No.	(%)	No.	(%)
MAMMALIA								
Unidentified	28	(16.7)	8	(6.9)	3	(4.0)	3	(5.8)
Marsupialia								
Didelphidae (opossums)	7	(4.2)						
Chiroptera								
Unidentified	2	(1.2)						
Emballonuridae (sac-winged bats)			2	(1.7)				
Primates								
Unidentified			1	(0.9)				
Hominidae (man)	1	(0.6)	1	(0.9)			2	(3.9)
Cebidae (monkeys)	1	(0.6)						
Callithricidae (marmosets)	1	(0.6)	1	(0.9)				
Edentata								
Unidentified	5	(3.0)	1	(0.9)	4	(5.3)	5	(9.6)
Bradypodidae (sloths)	47	(28.0)	13	(11.2)			9	(17.3)
Myrmecophagidae (anteaters)	22	(13.1)			3	(4.0)	4	(7.7)
Dasypodidae (armadillos)	4	(2.4)	2	(1.7)	57	(76.0)	11	(21.2)
Lagomorpha								
Leporidae (rabbits)	14	(8.3)	10	(8.6)	7	(9.3)	2	(3.9)
Rodentia								
Unidentified	2	(1.2)						
Erethizontidae (porcupines)	19	(11.3)	5	(4.3)			1	(1.9)
Cricetidae (rice rats)							1	(1.9)
Muridae (common rats)	1	(0.6)						
Echimyidae (spiny rats)	1	(0.6)						
Hydrocoeridae (capybara)							1	(1.9)
Carnivora								
Unidentified							1	(1.9)
Musterlidae (weasels, skunks)	2	(1.2)						
Canidae (dogs, foxes)	2	(1.2)						
Perissodactyla								
Unidentified (horses, tapirs)	2	(1.2)					1	(1.9)
Artiodactyla								
Unidentified	1	(0.6)						
Bovidae (cows)	2	(1.2)	1	(0.9)			2	(3.9)
AVES								
Unidentified	1	(0.6)					1	(1.9)
Galliformes								
Cracidae (curassows, guans)	1	(0.6)						
Phasianidae (chickens, quails)	1	(0.6)						
REPTILIA								
Unidentified			48	(41.4)	1	(1.3)	6	(11.5)
Sauria (lizards)			17	(14.7)			1	(1.9)
Serpentilia (snakes)			3	(2.6)			1	(1.9)
Chelonia (turtles)			3	(2.6)				
AMPHIBIA								
Unidentified	1	(0.6)						
Total blood meals identified	168	(100)	116	(100)	75	(100)	52	(100)

lo, another armadillo, an unidentified mammal and a spiny rat, respectively.

In the tree buttress, bioptope members of the order Edentata, which include sloths, armadillos and anteaters, provided 52.5% of the total blood meals identified from the 18 sandfly species studied.

Sloth infection rates

As a result of a previous investigation, it had been determined that biopsies from the spleen and nose of sloths yielded more *Leishmania* isolates in culture than any of the many tissues routinely examined;[6] therefore, we cultured only these two tissues. *L. braziliensis* was isolated from 6 of 26 (23.1%) *C. hoffmanni* captured in El Aguacate and 8 of 42 (19.0%) *C. hoffmanni* taken in the Mojinga Forest. The parasites were isolated from the spleen of all 14 and the nose of only three animals.

DISCUSSION AND CONCLUSIONS

Lutzomyia triramula and *Lu. camposi* are non-anthropophilic species more closely associated with animal burrows than with tree buttresses. Animal burrows frequently are built beneath the root systems of large trees, and in such instances *Lu. triramula* is often encountered in large number in buttresses associated with the burrows. Blood-meal identifications showed that armadillos were the predominant hosts of *Lu. triramula* and *Lu. camposi*.

L. ovallesi is a man-biter, but as yet has not been implicated as a vector of *Leishmania*. The most frequent hosts for this species found in our study were armadillos and sloths. *L. ovallesi* should be considered as a potential vector of *Leishmania* because of its feeding habits and density in tree buttresses.

L. ylephiletor, *Lu. shannoni* and *Lu. trapidoi* comprised 54.5% of the phlebotomine fauna collected from tree buttresses and 77.1% of the blood-engorged females in which vertebrate hosts were identified. The fact that sloths were the hosts of 553 of 1,228 (45.0%) of these species in the tree-buttress biotope emphasizes the importance of these sandflies in the epidmiology of leishmaniasis among the edentates. *C. hoffmannii*, the principal reservoir of *L. braziliensis* in Panama, was identified as the host of all 52 Bradypodidae positive blood meals tested with genus-specific sloth antisera. This is not surprising since most of our sandfly collections were made in heavily forested areas, and *B. infuscatus* is most commonly encountered in secondary growth vegetation or areas where such flora interdigitates with primary forests. *L. ylephiletor* and *Lu. trapidoi* are anthropophagic vectors and will readily feed on man in the vicinity of tree buttresses. Although *Lu. shannoni* is not anthropophilic, its frequent feedings on sloths probably result in its playing an important role in the transmission and maintenance of *Leishmania* among these animals.

This work extends the observations reported by Tesh et al.[13,14] who conducted two similar studies in El Aguacate and Limbo, central Panama. Their investigations, which provided the first definitive results of sandfly feeding proclivities in the New World, were somewhat limited in that host identifications were not obtained below the class and ordinal levels of taxonomic specificity. Excluding one of the two El Aguacate sites, which was biased by the presence of sentinel monkeys and rodents, these workers showed that *Lu. ylephiletor, Lu. trapidoi* and *Lu. shannoni* fed primarily on edentates.[13] In their subsequent study, *Lu. ylephiletor* and *Lu. trapidoi* again showed an apparent predilection for edentates; however, rodents were the most frequent host of *Lu. shannoni*.[14]

The overall leishmanial infection rate of sloths in Panama has been reported as 19.3% and is known to reach 68.8% in highly endemic areas.[6] These data, and the elucidation of the feeding habits of sandflies cohabiting the same sylvatic biotope as sloths, presented in our study, indicate that tree buttresses and their immediate surroundings are high risk areas for *Leishmania* transmission. Activities which may result in man's encroachment into tree-buttress biotopes include the clearing of land by farmers for crop planting, logging operations, hunting, road building, dam construction, and military jungle training missions.

Recently, Chaniotis et al.[15] reported a 20.6% mean reduction of anthropophagic sandflies in the Mojinga Forest in a 1-year study during bimonthly sprayings of tree trunks with 2% malathion emulsifiable concentrate. Such control measures may be feasible on a limited scale for some of the high risk activities cited above.

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