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Enzootic cutaneous leishmaniasis in eastern Panama

III. Ecological factors relating to the mammalian hosts

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The Gorgas Memorial Laboratory conducted an intensive field programme from September 1968 to June 1969, investigating leishmaniasis in a locality of eastern Panama. Parasitological findings were reported by Herrer *et al.* (1971), and entomological studies by Christensen *et al.* (1972).

This paper presents data on habitat distribution and relative abundance of the commoner mammal species encountered, several of which were shown in the accompanying studies to be of importance in the epidemiology of cutaneous leishmaniasis in this region of Panama.

The programme was conducted at Sasardi, an area in which a former base camp had been erected by the Interoceanic Canal studies programme during the survey of proposed route 17 for a new sea-level canal across the isthmus of Panama. Sasardi Camp is located in San Blas Territory, eastern Panama, approximately 5·5 km E of Mulatupo Island. An Indian trail ('Mulatupo trail') leads inland, approximately southwest in direction. This trail continues beyond the Sasardi Camp, crosses the Cordillera de San Blas into Darien Province, and eventually reaches and proceeds beyond the Cuna village of Morti.

Description of study area. The area around Sasardi was originally moist tropical forest but in the vicinity of Mulatupo a strip of up to 5 km in width, paralleling the coastline, has been disturbed, mainly by agricultural activities, for many years. Three plant associations can be distinguished in the study area: (i) agricultural (coconut plantation) (ii) secondary forest succession from former agricultural land, and (iii) primary forest. The coconut plantation (Plate XXIV, Fig. 1) extends inland from the beach for about 1 km. This area is distinct ecologically in that it is fairly well tended by the Cunas, and there is little woody underbrush. Water accumulates on the surface of the ground during the wet season. The soil and tree bases are pocked with holes excavated by land crabs. Toward the west the coconut stand interdigitates with an old cacao plantation (Plate XXIV, Fig. 2). This area has abundant undergrowth and is poorly tended by the Cunas; succession to secondary forest is well advanced and forms a fairly thick canopy overhead. It is rather a broad area running 1 to 2 km inland from the coconut plantation. The camp is located in a recently disturbed area that was once corn and rice fields surrounded and interlaced with banana plants. Secondary growth in this locality is also well advanced. Remnants of former agricultural crops provide an abundance of ecotonal interfaces with successional vegetation (Plate XXV, Fig. 3). *Heliconia* flourishes in the more open areas, occasionally forming dense thickets (Plate XXV, Fig. 4). The unbroken primary forest begins about 1300 m W of

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the campsite. In this area the river Cuadi (Rio Sasardi) has formed a broad curve in its flow from the west toward the coast, providing a southern and eastern border for the campsite. Remnants of original primary forest (Plate XXVI, Fig. 5) line the river edge.

Animals were trapped from the vicinity of the beach and coconut plantation in the east to a section well within the primary forest west of the base camp. However, the greatest trapping effort was concentrated in the secondary forest surrounding the campsite, within an area of approximately 250000 m². This was most intensively trapped because it was here that the rice rat, *Oryzomys capito*, was found infected with *Leishmania* at the outset of our studies.

Extensive flooding occurred in May 1969, just before the June field trip, which markedly altered the nature of the forest floor. Swift water swept clean some sites near the camp, removing the leaf litter and debris which had accumulated. Information on the frequency of such floods is not available, but local Indians informed us that the last similar sweeping action of floodwaters had occurred about four years previously. The topography of this section is relatively flat and low, with the 30 m contour line passing through the campsite, so such floods are probably a recurrent phenomenon in exceptionally wet years.

MATERIALS AND METHODS

Collection of Mammals

Small mammals were collected live with traps of three sizes: small Sherman traps, wire traps $41 \times 14 \times 14$ cm, and $78 \times 20 \times 20$ cm (National Live Trap Corporation). The largest traps were used only for arboreal mammals. Traps were usually baited with banana and corn, and occasionally with toasted coconut. Arboreal trapping was limited to those trees which possessed certain characteristics that indicated a higher probability of use by mammals, such as broad, interlocking branches, heavy vine growth, or tree holes. Traps were laid 5 to 15 m above ground in most cases. All traps were checked in the early morning, and rebaited and reset when necessary. As trap returns fell off in particular areas, traps were moved to adjacent untrapped sites. Hunting dogs were used in June 1969 in an attempt to collect certain burrow-inhabiting animals.

Criterion Used to Estimate the Results of Trapping

The term 'trap-night' is defined as one trap set per night. A trap success ratio was established for each plant association by dividing the number of trap-nights by the number of animals collected. The ratio represents the average number of trap-nights required to collect a single animal. Thus the lower the ratio the higher the trap success.

RESULTS

Mammals Collected

A total of 481 forest mammals belonging to 16 genera and 19 species was collected. Five of these animals, two *Agouti paca* and three *Dasyprocta punctata*, were captured with the help of dogs, and are not considered in the tables. Table I shows the mammalian species composition and density among the different plant associations during each of the periods sampled. Table II summarizes the total animal live-trap collections from Sasardi in relation to plant associations.

TABLE I

Mammals trapped within different plant associations at Sasardi during four collecting periods
The number of trap-nights in each habitat is shown in brackets

Species	14–22 September 1968				30 November 18 December 1968	5–16 March 1969		4–25 June 1969				Total (4139)
	Primary forest		Secondary growth		Secondary growth	Secondary growth		Primary forest	Secondary growth		Coconut plantation	
	Trees (46)	Ground (48)	Trees (56)	Ground (182)	Ground (1396)	Trees (238)	Ground (635)	Ground (246)	Trees (69)	Ground (1157)	Ground (66)	
Aotus trivirgatus ...						1						1
Bassaricyon gabbii ...						3						3
Caluromys derbianus ...			2	1		1						4
Didelphis marsupialis	1	1		1	1					2	1	7
Diplomys labilis ...						1						1
Marmosa robinsoni ...			1	7	21	2	12		3	6		52
Metachirus nudicaudatus				2	8		16	3		23		52
Nectomys alfari ...					1							1
Oryzomys capito ...				13	42		2			1		58
O. caliginosus ...							8			6		14
O. bicolor									1	1		2
O. alfaroi								1				1
Potus flavus						1						1
Proechimys semispinosus		2		14	70		71			76	1	234
Saguinus geoffroyi ...			8		4	12			7			31
Sylvilagus brasiliensis					1							1
Tylomys panamensis ...	1		3		4	1			3	1		13
Totals ...	2	3	14	38	152	22	109	4	14	116	2	476

TABLE II

Collecting effort and trap success among different plant associations during four collecting periods at Sasardi

	Primary forest		Secondary growth*		Coconut plantation	
	Trees	Ground	Trees	Ground	Ground	Total
Number of trap-nights ...	46	294	363	3370	66	4139
% of trap effort	1·1	7·1	8·8	81·4	1·6	100·0
Number of animals trapped ...	2	7	50	415	2	476
Trap success ratio†	23·0	42·0	7·3	8·1	33·0	8·7

* Includes former agricultural land in which secondary growth succession is well advanced.

† Trap success ratio $= \frac{\text{Number of trap-nights}}{\text{Number of animals trapped}}$

Arboreal trapping was done during the September, March and June sampling periods, and comprised 12·0% of the collection effort. Fifty-two mammals were collected in traps set in trees, whereas 424 mammals were collected in traps placed on the ground during the four trips.

The most ecologically diverse plant association was the rapidly maturing secondary forest where reclamation of former agricultural flora provided abundant habitats for a wide variety of animals. Five of the 19 species of mammals collected, *Proechimys semispinosus*, *O. capito*, *Marmosa robinsoni*, *Metachirus nudicaudatus*, and *Saguinus geoffroyi* comprised 90·6% of the total collection from this association (Table III).

The combined collections from primary forest and coconut plantation made up less than 10% of our trapping effort (Tables I, II) and are considered only briefly in the following discussion.

TABLE III

Species composition of mammals trapped in the secondary forest association arranged according to their abundance

Species	September 1968 (238)*		December 1968 (1396)		March 1969 (873)		June 1969 (1226)		Total (3733)	
	Animals trapped	%	Animals trapped	%	Animals trapped	%	Animals trapped	%	Animals trapped	%
P. semispinosus	14	(26·9)	70	(46·1)	71	(54·2)	76	(58·4)	231	(49·7)
O. capito	13	(25·0)	42	(27·6)	2	(1·5)	1	(0·8)	58	(12·5)
M. robinsoni	8	(15·4)	21	(13·8)	14	(10·7)	9	(6·9)	52	(11·2)
M. nudicaudatus	2	(3·8)	8	(5·3)	16	(12·2)	23	(17·7)	49	(10·5)
S. geoffroyi	8	(15·4)	4	(2·6)	12	(9·2)	7	(5·4)	31	(6·7)
Other 12 species	7	(13·5)	7	(4·6)	16	(12·2)	14	(10·8)	44	(9·4)
Totals	52	(100·0)	152	(100·0)	131	(100·0)	130	(100·0)	465	(100·0)

* Trap-nights

DISCUSSION

Relative Mammalian Densities in the Different Plant Associations Studied

Trap success was markedly greater in the secondary growth vegetation than in primary forest or in the coconut plantation (Table II). This supports visual observations which suggest that mammalian densities are lower in primary forest than in ecologically disturbed areas. The low density in the coconut plantation appeared to be the result of both the absence of woody underbrush and greater human activity. However the minimal trapping effort in this area invalidates further speculations.

Both the rice rat, *O. capito*, and the spiny rat, *P. semispinosus*, were found infected with *Leishmania* during the initial phase of this project in December 1968 (Herrer *et al.*, 1971). All of the infected rice rats were trapped in secondary forest succession of former corn, rice and banana crop land. This discovery naturally influenced our subsequent trapping efforts which were concentrated in this plant association. Overall, 3833 (90·4%) out of a total of 4239 trap-nights were devoted to secondary forest collections. Although the *P. semispinosus* population appeared relatively unaffected by the intensive trapping effort in this association, *O. capito* densities diminished markedly in March and June 1969 (Table I).

Species Potentially Most Important as Reservoir Hosts

The principal mammalian host of *Leishmania* in Sasardi appeared to be *O. capito* which showed an overall infection rate of 36%. (Herrer *et al.*, 1971). Four per cent of the dominant *P. semispinosus* were also found infected, which indicates that this animal may also play an important role in the ecology of the zoonosis in Sasardi. In addition, a single specimen each of the arboreal spiny rat, *Diplomys labilis*, the spotted agouti, *Agouti paca*, and the murine opossum, *M. robinsoni*, were found infected. The infection in the single arboreal spiny rat collected may indicate a high degree of susceptibility. However, it is a rather uncommon animal and therefore of doubtful importance to the maintenance of the zoonosis in nature. The discovery of the infection in one of the two spotted agoutis may prove more significant. Agoutis, highly sought after as game animals, are protected by law. They are fairly abundant and widely distributed throughout the Republic of Panama. The nature of their role in the ecology of leishmaniasis in Sasardi and the rest of the Republic has not been elucidated. The single infection found among 52 murine opossums indicates that this animal is probably an incidental host of the zoonosis in Sasardi. It should be emphasized that 99% of the sandflies attracted to the rice rat and spiny rat were *Lutzomyia olmeca*, the vector of *Leishmania* incriminated in this area (Christensen *et al.*, 1972). It is interesting that one arboreal animal exhibited *Leishmania* in a focus in which the zoonosis primarily affected terrestrial animals. However, the nocturnal foraging activities of several typically arboreal species in Sasardi frequently bring them into contact with the terrestrial environment. For example, five *T. panamensis*, four *S. geoffroyi* and 46 *M. robinsoni* were collected in terrestrial traps. It is during this phase of their activity that they are most likely to encounter *L. olmeca*. Christensen *et al.* (1972) showed that this sandfly vector is most active near ground level.

High leishmania infection rates among *O. capito* have been found in Brazil (Nery-Guimaraes *et al.*, 1966; Lainson and Shaw, 1968, 1969) and the sandfly *L. flaviscutellata*, a species closely related to *L. olmeca*, has been incriminated as the probable insect vector (Shaw and Lainson, 1968). It is suggestive that in certain localities of Brazil and Panama the

same vertebrate host and a similar species of insect vector are involved in the maintenance of enzootic foci of cutaneous leishmaniasis.

Sporadic aggregations in secondary forest habitats typify the distribution patterns of *O. capito* in Panama (*unpublished data*). Insular distribution patterns such as this account for the decimation of a population by intensive trapping methods such as those used by us at Sasardi. The implications of concentrated foci of highly susceptible animal species cohabiting the same locality as a vector species (Christensen *et al.*, 1972) are clear. This situation and the fact that leishmania infection in *O. capito* lasts a considerable length of time (Herrer *et al.*, 1971), seem responsible for the high infection rates frequently found in the rice rat.

SUMMARY

1. Ecological factors relating to the mammalian hosts of cutaneous leishmaniasis were studied in Sasardi, San Blas Territory, eastern Panama. This study involved intensive mammal collecting during each of four field trips between September 1968 and June 1969.

2. About 90% of the trapping effort was conducted in secondary forest and abandoned agricultural fields in which succession of secondary vegetation was well advanced. A large coconut plantation and primary forest accounted for the remaining 10% of the trapping effort. The population density of mammals was highest in the secondary forest association.

3. A total of 481 mammals belonging to 16 genera and 19 species was collected. The following five species comprised 90·6% of animals trapped in secondary forest or recently disturbed areas reverting to secondary growth, *Proechimys semispinosus* (49·7%), *Oryzomys capito* (12·5%), *Marmosa robinsoni* (11·2%), *Metachirus nudicaudatus* (10·5%) and *Saguinus geoffroyi* (6·7%).

4. The *P. semispinosus* population was relatively unaffected by the intensive trapping during the four field trips; however, the *O. capito* population diminished markedly after the second trapping period.

5. The rice rat *O. capito*, had a leishmania infection rate of 36% and appeared to be the principal mammalian host responsible for the maintenance of the zoonosis in the study area. Four per cent of the spiny rats, *P. semispinosus*, were infected also, and this animal may play an important role in the ecology of leishmaniasis at Sasardi. A single specimen each of the arboreal spiny rat, *Diplomys labilis*, the spotted agouti, *Agouti paca*, and the murine opossum, *Marmosa robinsoni*, were found infected. The relative importance of each animal in relation to the ecology of leishmaniasis in Sasardi is discussed.

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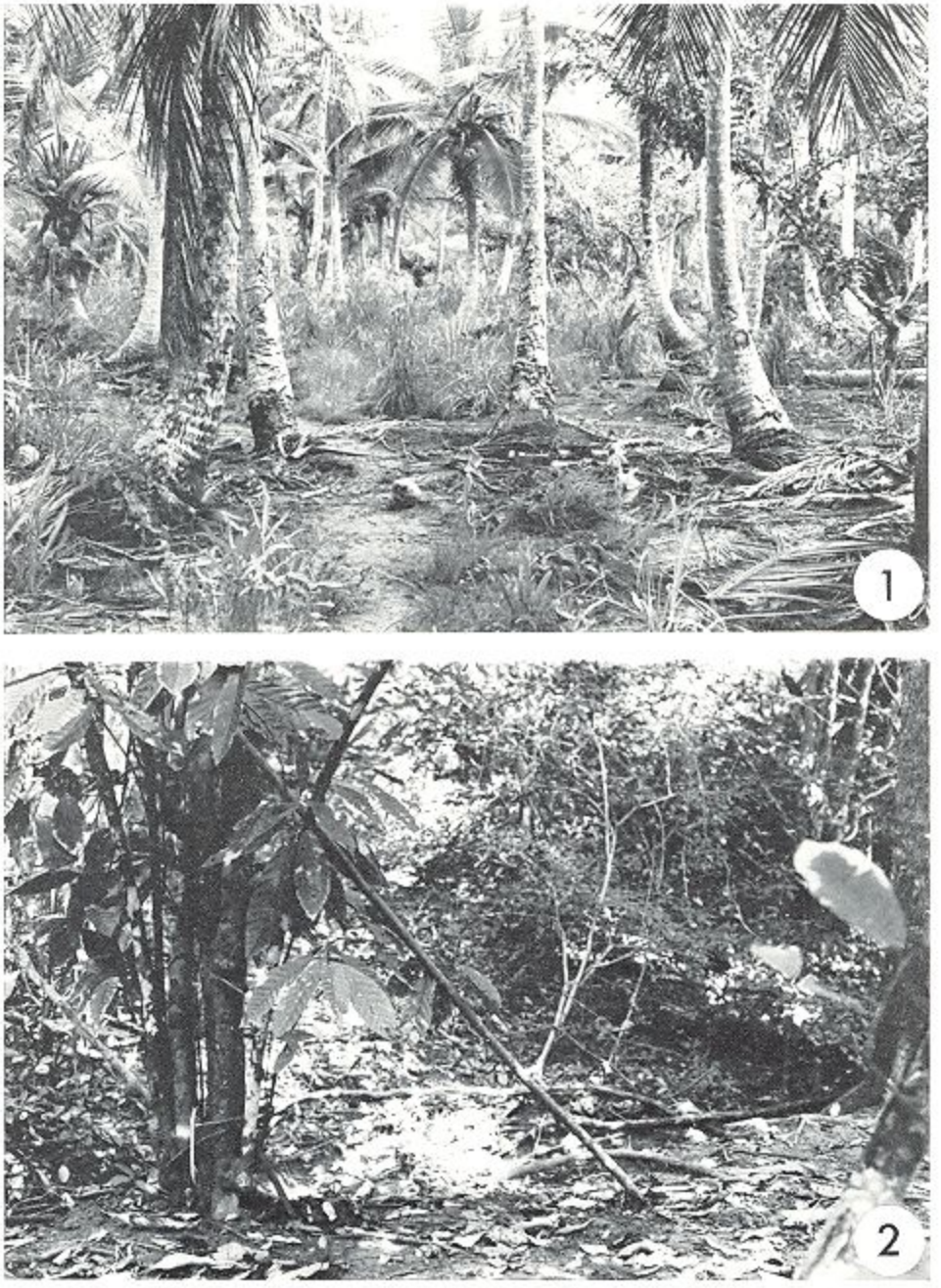

FIG. 1. Coconut plantation located near the coast is well tended by the Cuna Indians. Limited mammal trapping was conducted in this area.

FIG. 2. Old cacao grove, inland from the coconut plantation. Secondary growth succession is well advanced. The Indians do not actively cultivate this area, and mammalian densities are much greater than in the coconut plantation.

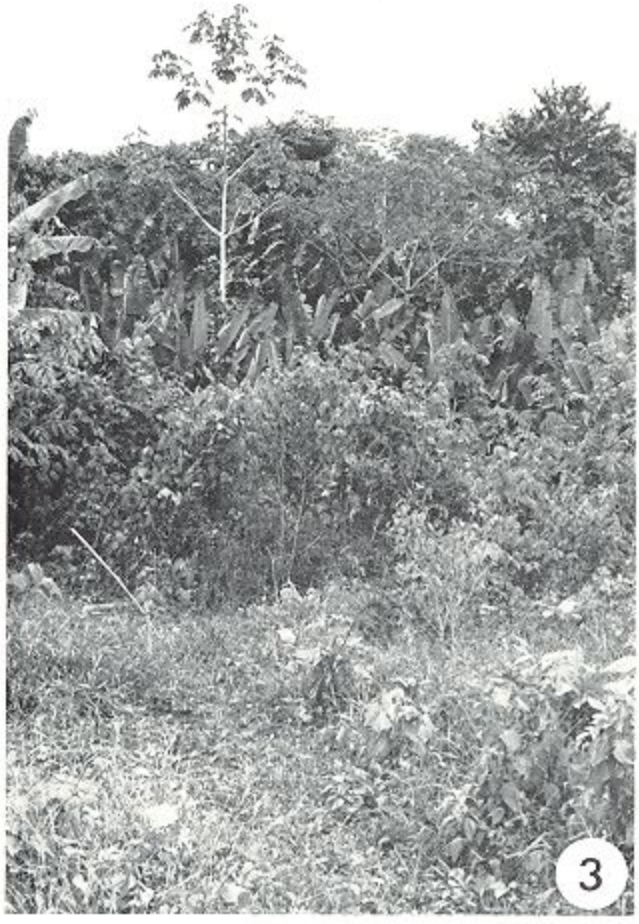

FIG. 3. Ecotonal interfaces of secondary growth in different stages of development. Rice rats (*Oryzomys capito*) with cutaneous leishmaniasis were trapped within this vegetational association.

FIG. 4. *Heliconia* thicket. Density of mammals in this plant formation was very low. Marsupials and, exceptionally, spiny rats (*Proechimys semispinosus*) were obtained in small numbers.

FIG. 5. Remnants of primary forest along the river's edge. *Leishmania* was isolated from a single *Diplomys labilis* trapped in this vegetational association.