Experimental transmission of the parasitic flagellates *Trypanosoma cruzi* and *Trypanosoma rangeli* between triatomine bugs or mice and captive neotropical bats

Maurice E Thomas/+, John J Rasweiler IV, Antonio D'Alessandro*

Department of Obstetrics and Gynecology, State University of New York Downstate Medical Center, Brooklyn, NY, 11203, US
*Department of Tropical Medicine, Tulane University School of Public Health and Tropical Medicine, New Orleans, LA, US

Trypanosoma cruzi *and* Trypanosoma rangeli*-like trypanosomes have been found in a variety of neotropical bat species. In this study, bats* (Artibeus lituratus, Carollia perspicillata, Desmodus rotundus, Glossophaga soricina, Molossus molossus, Phyllostomus hastatus) *were maintained under controlled conditions, and experiments were conducted to determine how they might become infected naturally with trypanosomes. All bats were first screened for existing infections by hemoculture and the examination of blood smears, and only apparently uninfected animals were then used in the experiments. Proof was obtained that the triatomine bug* Rhodnius prolixus *would readily feed upon some of the bats, and two species became infected after being bitten by bugs infected with* T. rangeli. *Some bats also became infected by ingesting* R. prolixus *carrying* T. cruzi*, or following subcutaneous or intragastic inoculation with fecal suspensions of* R. prolixus *containing* T. cruzi. P. hastatus *became infected after ingesting mice carrying* T. cruzi. *All of the bats studied inhabit roosts that may be occupied by triatomine bugs and, with the exception of* D. rotundus*, all also feed to at least some extent upon insects. These findings provide further evidence of how bats may play significant roles in the epidemiology of* T. cruzi *and* T. rangeli *in the New World tropics.*

Key words: *Trypanosoma cruzi* - *Trypanosoma rangeli* - triatomines - neotropical bats - Chagas disease

Bats are among the most abundant mammals in the New World tropics, and some are known hosts of *Trypanosoma cruzi* and a number of other trypanosomes. Despite the potential epidemiological significance of bats as reservoir hosts for these trypanosomes, information about their vectors, and specifically how infections might be obtained and spread, is mostly lacking.

In this study several common species of neotropical bats (*Artibeus lituratus, Carollia perspicillata, Desmodus rotundus, Glossophaga soricina, Molossus molossus, Phyllostomus hastatus*) were maintained under controlled conditions in captivity. Experiments were conducted to determine how the bats might become infected with trypanosomes naturally and the infections could then be transmitted to other organisms. This research was pursued in 1975/1976 at the NIH-sponsored, Tulane University, Universidad del Valle International Center for Medical Research in Cali, Colombia (D'Alessandro & Thomas 1975). For this reason, it was carried out before some modern molecular methods, which might now be utilized in such work, had become available. Nevertheless, the findings add important insights into how bats may be involved in the epidemiology of trypanosome-induced diseases in the New World tropics.

MATERIALS AND METHODS

Source and maintenance of bats - All of the bats used in these studies were captured in rural areas of the Departamento del Valle, Southwestern Colombia, around the city of Cali. The bats were either caught with hand nets in a variety of diurnal roosts (e.g., hollow trees, road culverts, abandoned mines, and houses) or with mist nets when the animals foraged at night. Only bats that were apparently healthy and not obviously pregnant were used in the experiments. The bats were then maintained in captivity at the Tulane University, Universidad del Valle International Center for Medical Research and Training. In brief, the *Carollia*, *Glossophaga,* and *Phyllostomus* were housed in bipartite cages of modest dimensions and fed fortified diets incorporating canned guava concentrate or sliced bananas as palatable bases (Rasweiler & Bonilla 1972, Rasweiler & Ishiyama 1973, Rasweiler 1975, 1977). Vampire bats (*D. rotundus*) which are solely sanguivorous were fed bovine blood that had been treated with sodium citrate and then frozen until the day of use (Quintero & Rasweiler l974). The *M. molossus* were fed mealworms. The bats were fed every night, except in an experiment involving *Phyllostomus* (see below).

Testing of bats for natural trypanosome infections - Before using bats in the captive experiments, all were first screened for preexisting trypanosome infections. This was done by hemoculture (using 5 ml of Tobie's biphasic medium and 0.02 ml of blood aspirated from the bat's heart per tube), as well as the examination of Giemsa-stained thick and thin blood smears. Only bats that did not show flagellates in these procedures were then used in the experiments described below. Several

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+Corresponding author present address: Department of Biology, Palm Beach Atlantic University, P.O. Box 24708, West Palm Beach, FL, 33416, US. E-mail: maurice_thomas@pba.edu

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of the isolated flagellates were also studied biologically in mice, tissue culture with Hela (human) or Vero (monkey) cells, and in *Rhodnius prolixus.*

Testing attractiveness of bats to R. prolixus - To test if *R. prolixus* would readily feed upon bats, some of these insects were placed in cages with the *Carollia, Glossophaga* or *Desmodus*. The cages were 35 cm × 23 cm × 15 cm. Each cage contained 1, 5 or 10 bats of a single species, plus 15 unfed *R. prolixus* (5 each of adults, 4th, and 5th instar nymphs). The bugs were left in the cages for about 24 h. The bugs were weighed before and after their exposure to the bats, and records of the nymphs' molting were kept. The bugs were clean, and the bats had previously been determined to be ‘uninfected’ when screened.

Experimental efforts to infect bats with T. cruzi - Only ‘uninfected’ bats that had adapted to captivity were used in these experiments. The animals were fed every night until the experiments were begun.

In the case of *Artibeus, Carollia, Glossophaga,* and *Molossus*, the bats were allowed to feed the night before. Each was then gently (loosely) restrained by hand and offered *T. cruzi*-infected *R. prolixus* with forceps. Although there was sometimes a reluctance to accept the first bug, subsequent ones were usually taken more readily. The bats were never force-fed. Interestingly, when this was done with *Carollia* or *Glossophaga,* the bats would furiously chew on each insect and remove most of its soft portions. The exoskeletons would then be flung aside with rapid movements of the bats’ heads, as previously reported (Ayala & D'Alessandro 1973).

For this experiment, clean *R. prolixus* had been infected with the lethal-for-mice Tulahuen strain of *T. cruzi*. This was done by feeding the bugs a suspension of mouse blood containing trypomastigotes through a latex membrane (condom). Each bat was then allowed to ingest from one to eight live, infected bugs.

Three other techniques for infecting bats with *T. cruzi* were also tried. Some omnivorous *Phyllostomus* were deprived of food for one night and then offered a mouse about to die of an acute *T. cruzi* infection. Control *Phyllostomus* were instead offered non-infected mice. Finally, some *Carollia* and *Glossophaga* were inoculated subcutaneously or by gastric tube with *T. cruzi*-infected feces from *R. prolixus*. To conduct these experiments, *R. prolixus* were confined to vials positioned up against the ventral surfaces of mice. The *R. prolixus* were permitted to feed on mice, and the bugs' feces were collected in the bottom of the vials (D'Alessandro 1972). The feces were then pooled and suspended in physiological saline. Finally, 0.02 ml of the suspension was injected sc, or 0.06 ml was inoculated by gastric tube, into the bats. These experiments were intended to mimic either the invasion of triatomid bites on the bats by infective, fecal metatrypomastigotes or the ingestion of infected *R. prolixus*. ‘Non-infected’ bats and *T. cruzi*-inoculated laboratory mice served as controls in these latter experiments.

To determine if the experimental and control animals had trypanosome infections, blood was drawn from them at days 2, 21, and 30 after the start of these studies. Hemoculture was then conducted as described above.

Transmission of T. rangeli to bats - The transmission of *T. rangeli* to bats was tested using a biologically-proven isolate originally obtained from an infected, brown capuchin monkey (*Cebus paella*). The flagellates were maintained as follows: first, a clean mouse was infected by the bite of *R. prolixus* with positive salivary glands; flagellates from a positive hemoculture of the mouse were then inoculated into the hemocoele of a new group of clean vectors, leading to the invasion of the salivary glands of most (79%) of the insects by *T. rangeli*. It had previously been determined that infected *R. prolixus* can then pass *T. rangeli* by bite to most exposed mice (D'Alessandro et al. 1986, D'Alessandro & Hincapie 1986). Captive, uninfected *Carollia* or *Glossophaga* were then exposed successively to two of these *R. prolixus* contained in a vial placed against the shaved, ventral surface of each bat. The bugs were closely observed and removed only after feeding upon the bats for a while. Feeding was then interrupted, and the bugs were allowed to feed upon a clean mouse. Finally, the bugs were autopsied and their salivary glands checked for trypanosomes. The bugs were not considered to be infective unless the mice subsequently tested positive for *T. rangeli* upon hemoculture, and the bugs' salivary glands were found to contain trypanosomes. The bats and the mice were checked for evidence of infection with *T. rangeli* by hemoculture at days 8, 21, and 30 after being fed upon by infective *R. prolixus*.

All of the animal experimentation was conducted prior to any national law in Colombia governing care and use of laboratory animals. However, the work was conducted humanely, using methods that would easily meet legislation of this type.

Roosting habits of bats in the wild - Two of us (MET and JJR) have worked extensively with the bat species discussed in this paper in Colombia, Panama, and/or Trinidad. This has included numerous visits to diurnal roosts to catch the following species for the establishment and restocking of captive breeding colonies, reproductive studies, or to harvest embryos for developmental studies: *C. perspicillata* (Rasweiler & de Bonilla 1972, Rasweiler & Badwaik 1996, 1997, Chen et al. 2005, Cretekos et al. 2005); *G. soricina* (Rasweiler & de Bonilla 1972, Rasweiler 1973, 1975); *D. rotundus* (Quintero & Rasweiler 1974). Observations were made on some of the diurnal roosting habits of *A. lituratus* in areas where this species was collected for the same purpose by mist-netting (Rasweiler & Ishiyama 1973). Observations on the roosting habits of *M. molossus* in Colombia were made when checking or collecting from roosts occupied by this species and frequently another bat of interest, *Noctilio albiventris* (Rasweiler 1978). Observations on the roosting habits of *P. hastatus* were made in the course of visits to caves, tunnels, and buildings on Trinidad, that were also frequently occupied by *C. perspicillata*, *G. soricina,* and/or *M. rufus* (also frequently referred to as *M. ater*; Rasweiler1988).

Voucher specimens - Voucher specimens for each of the species worked with have been deposited in the United States National Museum (USNM). These were collected prior to the studies described in the present paper, but in the same area. They constitute part of the almost 2000 specimen Arata/Thomas collection of bats collected by one of the authors of the present paper (MET) in the Cali, Colombia, area and donated to the USNM. The species, sex, and USNM numbers are: *C. perspicallata* ♂446624, ♀483434; *D. rotundus* ♂447636, ♀447635; *A. lituratus* ♂447405, ♀447404; *G. soricina* ♂446461, ♀446457; *P. hastatus* ♂483345, ♀446419; *M. molossus* ♂447707, ♀447710.

RESULTS

In this study uninfected *R. prolixus* were caged for about 24 h with bats of three different species (*Carollia*, *Glossophaga*, and *Desmodus*). All of the *R. prolixus* could be accounted for at the end of this period, and no bug remains were found in any of the cages. Clear evidence was obtained that a number of the *R. prolixus* had fed upon the bats. This was indicated by a gain in weight by many of the bugs while housed with the bats and by nymphs molting within 15 days of the feeding. Molting is normally stimulated by the body distention caused by a full meal. In the experiment with *Glossophaga*, half of 40 *R. prolixus* (adults, 4th, and 5th instar nymphs) fed upon the bats. Furthermore, 40% (8/20) of the nymphs molted. Similar results were observed with the bugs housed with *Desmodus*. Finally, 14 of 19 *R. prolixus* caged with *Carollia* consumed a full blood meal.

Due to time constraints, the ability of infected *R. prolixus* to transmit *T. cruzi* to bats under such circumstances was not assessed. However, the experimental transmission of *T. cruzi* to bats by several other routes was successful in most cases (Table I). When *R. prolixus* carrying *T. cruzi* were ingested, the following infection rates were observed: 3/10 *Carollia*, 2/8 *Artibeus*, 2/14 *Molossus*, and 3/6 mice. Curiously, all *Glossophaga* failed to show infection after ingesting *T. cruzi*-infected *R. prolixus*. These negative results cannot be readily explained, as *Glossophaga* was susceptible to infection by other means and frequently carries *T. cruzi* in the wild (see below). Seven of 20 *Phyllostomus* also became infected by eating live, *T. cruzi* infected mice. The subcutaneous or intragastric inoculation of a fecal suspension containing *T. cruzi* successfully infected *Carollia*, *Glossophaga*, and mice. All of the non-inoculated, control bats failed to exhibit any evidence of *T. cruzi* infections, when their blood samples were subjected to hemoculture.

The results of attempts to infect bats with *T. rangeli* by bites of infected *R. prolixus* are presented in Table II. The duration of infection was also assessed by hemoculture at different time intervals after exposure to the *R. prolixus*. Three *Carollia* were each bitten by two infective *R. prolixus*. All three were positive up to day 36, and 2/3 were positive until day 138 after the infective bites. All four control *Carollia*, bled at the same time intervals, were found to be negative. Only one of four inoculated *G. soricina* was found to be positive, when their blood samples were subjected to hemoculture between six and 12 days.

The roosting habits in the wild of the bat species worked with in this study are listed in Table III. In most cases, bats were repeatedly observed roosting in many of the indicated sites by two of the authors of this paper.

TABLE II

Trypanosoma rangeli transmission by *Rhodinus prolixus* bite

Species of animal bitten by *R. prolixus*	Positive hemoculture at day 6-12	day 30-36	day 138
3 *Carollia*	3/3	3/3	2/3
3 mice	3/3	ND	ND
4 *Glossophaga*	1/4	0/4	0/1
3 mice	3/3	ND	ND
Non-bitten (controls)			
4 *Carollia*	0/4	0/4	0/4
1 *Glossophaga*	0/1	ND	ND

ND: not done.

TABLE I

Experimental infection of bats with *Trypanosoma cruzi*

Animal species (feeding habits)	Type of inoculations: Infected fecal suspension: Subcutaneous	Gastric	Ingestion of infected organisms: Bugs	Mouse	Non-inoculated
Carollia (fru, nect, insec)	2/2	2/2	3/10	ND	0/14
Glossophaga (fru, nect, poll, insec)	2/2	2/6	0/13	ND	0/6
Artibeus (fru, nect, poll, insec)	ND	ND	2/8	ND	0/18
Molossus (insec)	ND	ND	2/14	ND	0/2
Phyllostomus (fru, flor, insec, verteb)	ND	ND	ND	7/20	0/7
Mouse	9/9	9/15	3/6	ND	ND

flor: floral parts; fru: fruits; insec: insects; nect: flower nectar; poll: pollen; verteb: smaller vertebrates; ND: not done.

TABLE III

Roosting habits of bats mentioned in text

Species	Roosting habits	References
Artibeus lituratus	In foliage of trees including palm trees[a], sometimes in buildings[b], under caves of buildings, hollow trees, well-lit caves	[a]Simmons & Voss 1998, [b]Bloedel 1954, present paper
Carollia perspicillata	Caves, abandoned mine and rail tunnels, active road tunnel, hollow trees, drain pipes and culverts, unused/abandoned buildings or rooms, attics, basements, under bridges, unused cisterns, darkened recesses in rock formations or stream banks	Present paper
Glossophaga soricina	Caves, abandoned mine and rail tunnels, hollow trees, drain pipes and culverts, unused/abandoned buildings or rooms, attics, basements, under bridges, unused cisterns	Present paper
Molossus molossus	Attics, spaces under roofs, hollow trees	Present paper
Phyllostomus hastatus	Under palm leaves[a], termite nests[b], dark caves, abandoned rail tunnel, unused/abandoned buildings, attics	[a]Goodwin & Greenhall 1961, [b]Santos el al. 2003, present paper
Desmodus rotundus	Deep narrow fissures[a], old wells, caves, mine tunnels, dark culverts, hollow trees, abandoned buildings	[a]Greenhall et al. 1983, present paper

DISCUSSION

In Colombia, thousands of bats have been examined for the presence of trypanosomes, and some of the results have been summarized by D'Alessandro and Barreto (1985). Twenty one species of bats were found to be infected with *T. cruzi* (*T. c. cruzi* and/or *T. c. marinkellei*), and the average rate of infection was about 9% (335/3709). These bats exhibited a broad range of feeding preferences (fruit, pollen and nectar, floral components, insects, smaller vertebrates or blood). Furthermore, they were collected both inside and outside of human dwellings. The most frequently infected were as follows: *A. lituratus* (predominantly frugivorous, 12% of 283); *C. perspicillata* (predominantly frugivorous, 11% of 907); *D. rotundus* (solely sanguivorous, 8% of 654); *G. soricina* (predominantly frugivorous, nectarivorous, and pollenivorous, 15% of 436); *M. molossus* (solely insectivorous, 12% of 379); and *P. hastatus* (omnivorous, 50% of 46). It was also observed that the frequency of infection varied significantly between some bat roosts.

Although *Artibeus*, *Carollia*, and *Glossophaga* generally feed on plant sources, it is clear that they also frequently consume significant quantities of insects (Arata et al. 1967, Fleming et al. 1972, Howell 1974, Howell & Burch 1974, rev. by Rasweiler 1975, 1977, rev. by Gardner 1977, Zortea 2003, Mello et al. 2004). This may be necessary to meet some of the bats' nutritional requirements (Rasweiler 1977). Furthermore, at least in the case of *Carollia* and *Glossophaga*, quantitative estimates and identification of the species consumed are complicated by the propensity of the bats to discard much of the insects' chitinous exoskeletons (Ayala & D'Alessandro 1973), as well as the bats' rapid gastrointestinal tract transit times (less than 2 h in some cases).

When *Carollia*, *Glossophaga*, and *Desmodus* were experimentally housed for about 24 h with *R. prolixus* in this study, clear evidence was obtained of the bugs feeding upon the bats. Although none of these *R. prolixus* carried *T. cruzi*, it seems likely that infected triatomines could transmit trypanosomes to the bats in the course of feeding activities. It is well-established that excretions from the bugs' Malphighian tubules, as well as their post-prandial feces, can contain infective metatrypomastigotes. These may then enter the mammalian host through the skin, conjunctiva or gastrointestinal tract. When suspensions of *T. cruzi*-infected feces from *R. prolixus* were inoculated into *Carollia* and *Glossophaga* via subcutaneous injection or gastric tube, many of the bats became infected.

As *Carollia*, *Glossophaga*, *Phyllostomus*, and *Molossus* have often been observed roosting in buildings, including those occupied by humans (Table III), the frequent transmission of *T. cruzi* therein between bats and humans via triatomine vectors seems quite feasible. *A. lituratus* occasionally frequents buildings, but more commonly roosts in trees (e.g., bananas and palms) which may be close to buildings. Palm trees are known to sometimes be infested with triatomines (Barreto et al. 1964, Whitlaw & Chaniotis 1978, D'Alessandro et al. 1971, 1984, Romana et al. 2004, Vasquez et al. 2004, Abad-Franch et al. 2005). Thus, *Artibeus* might also be a significant reservoir host for *T. cruzi* transmissible to humans. Brief comments in the literature indicate that

Phyllostomus and *Molossus* sp. sometimes roost in palm trees as well (Goodwin & Greenhall 1961, Jennings et al. 2000, 2002). Reports of bats roosting in palms may be rare, because this behavior is difficult to observe and species' identifications would often be challenging. Vampire bats (*Desmodus*) commonly roost in hollow trees, caves, mine tunnels, and dark culverts and presumably may be fed upon by *T. cruzi*-infected triatomines in some of these locations.

Some *Carollia* and *Glossophaga* were housed experimentally with *R. prolixus* infected with *T. rangeli*, and several bats contracted trypanosome infections via bites by the bugs. This study apparently represents the first successful transmission of *T. rangeli* infections to bats and confirms an earlier observation that they can host *T. rangeli*-like trypanosomes (Marinkelle 1966, D'Alessandro 1976). *T. rangeli* has also been found in a large variety of other mammalian hosts, ranging from mice to horses.

It was also experimentally established in this study that several bats could become infected with *T. cruzi* through the ingestion of infected *R. prolixus* (*Carollia*, *Artibeus*, and *Molossus*) or mice. Although it was possible that some of the infections observed in these studies were already present when the bats were captured (but undetected by the screening procedure), this would seem to be an unlikely explanation for all of them. In fact, control animals consistently tested negative, and only experimentally-infected bats ever tested positive.

These findings clearly raise the possibility that some of these bats might contract *T. cruzi* naturally through the capture and consumption of infected prey. Wood (1952) previously suggested that some trypanosome infections in Californian bats may be acquired by the ingestion of infected *Triatoma* by the bats while flying, and other carnivores are known to contract trypanosome infections from their prey (Yeager 1971). The notably high rate (50%) of preexisting *T. cruzi* infections observed in Colombian *Phyllostomus* may be partially attributable to the fact that this bat is omnivorous and sometimes consumes smaller mammals (Dunn 1933). There have also been many reports of *P. hastatus* (or presumed *P. hastatus*) feeding in part upon insects (rev. by Gardner 1977, Willig et al. 1993).

One must consider as well the possibility that some of the infected triatomines consumed may not be in flight. Insects were a favorite food of captive *G. soricina* maintained in an outdoor flight cage in El Salvador. Some of the insects were caught while at rest on the cage screening or were nonvolant species gleaned from low-growing vegetation by hovering bats (Felten 1956). *G. soricina* is highly adept at hovering (e.g., to feed in part upon night-blooming flowers), while *C. perspicillata* has a somewhat more limited capability to hover (e.g., to pluck fruit with its mouth or feet; Fleming 1988).

With respect to the oral transmission of trypanosome infections, it is also pertinent to mention the role of vampire bats (*Desmodus*) in the epidemiology of *T. hippicum* (= *T. evansi*), the agent responsible for murrina in horses and cattle. These trypanosomes multiply in the bat's blood, as they do in the blood of natural vertebrate hosts. Furthermore, there are occasions in which the oral mucous membrane of *Desmodus* apparently presents no barrier to the parasites, enabling them to pass through in both directions during the course of the bat's feeding activities. Thus, the vampire bat can function as both a host and a vector of this disease. This presents a rare example of a blood parasite commonly being transmitted directly from one mammal to another (Hoare 1965). Although vampires can be hosts of *T. cruzi*, it is presumed that they cannot also be vectors for this parasite. *T. cruzi* normally multiplies in the tissues of the host, and parasitemia is very low. Opossums reportedly maintain a high parasitemia, however, for as long as the infection is present (Hoare 1972). If the same thing occurs in vampires, they could conceivably function as vectors for this disease as well.

Observations that *D. rotundus* and several other bats included in the present study can contract trypanosome infections via oral routes raises the possibility that this might also occur if fresh *T. cruzi*-infected feces from triatomines are ingested in the course of grooming activities. *C. perspicillata* and *G. soricina* have been observed grooming themselves (Howell & Hodgkin 1976, Williams, 1986, Fleming 1988). Female *P. hastatus* and *D. rotundus* will groom each other (social grooming), as well as their young (Wilkinson 1986).

The current findings provide further evidence of how bats may be playing significant roles in the epidemiology of *T. cruzi* and *T. rangeli* in the New World tropics. This could contribute to a better understanding of how *T. cruzi* occasionally moves from sylvatic settings to initiate new domestic transmission cycles of Chagas disease (see Dias et al. 2002).

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