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Source: Journal of Wildlife Diseases, 6(4) : 313-322

Published By: Wildlife Disease Association

URL: https://doi.org/10.7589/0090-3558-6.4.313

Animals as Reservoir Hosts of Human Trypanosomes

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Abstract

Present knowledge on reservoir hosts of *Trypanosoma rhodesiense*, *T. gambiense* and *T. brucei* in Africa and *T. cruzi* and *T. rangeli* in America and experimental transmission studies of *T. cruzi* in mammalian hosts and in lizards is discussed. The difficulty in differentiating the African species of human trypanosomes, which appear not to be host specific, is a major obstacle to epizootiological studies.

Introduction

Trypanosomiasis is still an important disease of livestock and man in the world. Human trypanosomiasis is mainly restricted to the tropical and sub-tropical regions of Africa and the Americas.

African trypanosomiasis due to *Trypanosoma rhodesiense* and *T. gambiense* was a widely spread fatal human disease at the beginning of the century. According to Buxton[6] an epidemic in Uganda in 1902-1905 killed 200,000 people. Since then the disease has been under control due to reduction of sources of infection, the protection of man from infection and the control of the vectors. In spite of this constant vigilance it persists at an irreducible level with occasional outbreaks. Wild game and domesticated animals can and are infected with these trypanosomes, but the importance of these animals as reservoir hosts is uncertain. This is because there is no practical way to distinguish *T. brucei* from *T. rhodesiense* and *T. gambiense* if an isolation is made from an animal.

In Central and South America human trypanosomiasis is caused by *T. cruzi* and it is considered by Koberle[37] the most frequent and dangerous plague of the American continent. It is frequent because of the large number of vectors and animal reservoir hosts and it is dangerous because as yet there is no effective treatment for it. The exact incidence of *T. cruzi* infection is not known, but it is estimated that there were at least — 7 million infected individuals.[56] Another trypanosome that infects man and animals in Central and South America is *T. rangeli*. Its pathogenicity in man is uncertain because dual infections with *T. cruzi* are not uncommon. Generally, the incidence in man and animals is high in most areas where it has been reported.

Our chief concern in the present communication is to summarize some of the work which deals with animals (both domestic and wild animals) that are or could be reservoir hosts of human trypanosomes.

African Trypanosomiasis

Human trypanosomiasis in Africa is found in an area between the southern limits of the Sahara and about 20° latitude.[58] Since the trypanosomes are transmitted by tsetse flies of the genus *Glossina*, the distribution of the disease is confined largely to areas where the vector can survive and breed.

Since *T. rhodesiense*, *T. gambiense* and *T. brucei* are morphologically identical and all three trypanosomes can infect animals, the only way to distinguish the two human trypanosomes from *T. brucei* when isolated from an animal is by inoculation into human volunteers. This method is both impractical and hazardous because of the possible occurrence of naturally drug resistant strains. This is further complicated by the fact that some humans are refractive to infection e.g. in the well-known Tinde experiment with a human strain of *T. rhodesiense*, approximately one half of the 336 human volunteers tested failed to become infected.[25] Because of these factors the study on the extent of animals as reservoir hosts is rather limited.

T. rhodesiense

The disease caused by *T. rhodesiense* is largely confined to hunters, fishermen, travellers and gatherers of beeswax. In the hot dry season human infections may be increased due to the combined effects of occupations leading man into the bush and high temperatures increasing the fly population.

(i) *Natural infections.* Evidence of a wild game reservoir for *T. rhodesiense* has been until recently circumstantial.[31] The first demonstration of *T. rhodesiense* from a naturally infected bushbuck was made by Heisch *et al.*,[32] the strain produced the clinical disease in a human volunteer and had the same drug response as that of *T. rhodesiense*. More recently Onyango *et al.*[33] isolated three *T. brucei*-like trypanosomes from domestic cattle. He was able to infect man with one of the three isolates and he believed this was *T. rhodesiense*. Besides domestic and wild animals, man himself can act as "healthy carriers" where the infection is asymptomatic. Such carriers are scarce and have only been reported from the southern borders of Rhodesia.[4]

(ii) *Experimental infections. T. rhodesiense* can infect all of the common laboratory animals. In a study on the experimental infection of African wild animals Ashcroft *et al.*[2] pointed out that wild animals can be arranged into two groups — those which are usually killed and those which are tolerant. Animals which are usually killed are not fed upon to any great extent by tsetse flies in nature and include Thomson's gazelle, dikdik, blue forest duiker, jackal, ant bear, hyrax, several cat and monkey. Tolerant hosts e.g. the common duiker, eland, bohor reedbuck, spotted hyena, oribi, bushbuck and impala, are those which are habitually fed upon by tsetse flies. Some of the earlier work on experimental infections of wild animals are summarized in Table 1.

Domestic animals e.g. sheep, goats, cattle, dogs, and cats can also be infected and these may serve also as reservoir hosts as shown by Onyango's recent isolation. An excellent account of asymptomatic *T. rhodesiense* infection in zebu cattle is given by Wilde and French.[57]

T. gambiense

Since the vectors of Gambian trypanosomiasis are polyphagous riverine tsetse flies, the incidence rate is affected by the proximity of villages to the shores of rivers or lakes or to water holes where the flies breed. As with Rhodesian sleeping sickness the incidence is higher in males than females, principally because of occupational exposure.

TABLE I. *Experimental Infections of Wild Animals With* Trypanosoma rhodesiense.

Types of Infections	Animals	References
Type I—infection mild	*Phacochoerus aethiopicus*	8, 52, 2
—trypanosomes scanty in blood and could only be detected for a short period.	*Potamochoerus koiropotamus*	24, 52, 2
—not all animals inoculated became infected and none of the infected animals died from the infection.	*Hystrix africae australis*	8, 52, 2
Type II—infection mild	*Sylvicapra grimmia*	9, 10
—trypanosomes scanty in blood but could be detected for a long period.	*Tanrotragnus oryx*	10, 52, 2
—usually all inoculated animals became infected and some infected animals died from infection.	*Aepyceros melampus*	10, 2
	Redunca redunca	24, 26
	Ourebia ourebi;	24, 25, 26
	Crocuta crocuta;	24, 26
	Tragelaphus scriptus	2, 24, 25, 26
Type III—infection quite severe	*Gazella thomsoni*	10, 2
—trypanosomes numerous in blood at time of death; also trypanosomes could be found in the cerebrospinal fluid.	*Rhynchotragus kirkii*	9, 10, 2
	Cercopithecus aethiops	2, 10
—all animals inoculated became infected and animals usually died from infection.		
	Orycteropus afer	52, 5
	Felis serval	24
	Cephalophus caerulus melanorrheus	24
	Dendrohyrax spp	8

(i) *Natural infections:* According to current views there is no evidence of natural *T. gambiense* infection in wild animals. However, the persistence of Gambian sleeping sickness in spite of widespread pentamidine prophylaxis in the former French West Africa led Willet[55] to suggest that animals should be considered as possible reservoirs of infection for man.

Though *T. gambiense* has not been found in wild animals it has been recorded from naturally infected domestic animals. Denecke[20] inoculated himself with a trypanosome from a dog, developed a local lesion at the site of inoculation and became infected. This trypanosome was designated *T. gambiense.* Van Hoof[51] reported a natural infection in a dog and the reference suggests that the disease was mild.

(ii) *Experimental infection.* The possibility of domestic ruminants acting as reservoirs has been pointed out by some early workers[35,26] who found that the infection in sheep and goats died out after a few months. However, Duke's work[28] suggsts that some strains might be pathogenic to goats. He[22] infected reed buck and bushbuck with *T. gambiense,* and these two animals were still infected 15 and 22 months later. He[23] also found calves were quite resistant to infection, only one out of four calves could be infected and the infected animal showed no clinical signs. Fraser and Duke[31] showed that experimentally infected antelopes may remain in good health for over a year and that *Glossina palpalis* could be infected from them 315 days after inoculation. Besides sheep and goats, horses, cats, and dogs could be infected and monkeys *(Macacus, Cynomolgus,* and *Cercopithecus)* are very susceptible.[56] Van Hoof[51] infected domestic pigs, goats, and dogs by the bites of infected tsetse flies. In pigs the infection showed no clinical signs and the infection died out within a year. He suggested that pigs may serve as potential reservoir hosts.

American Trypanosomiasis

T. cruzi and *T. rangeli* infect man in Central and South America; both are transmitted by reduviid bugs and mixed infections are not uncommon e.g. in a study of 80 patients in Venezuela, 44% were infected with *T. rangeli,* 34% *T. cruzi,* and 22% with mixed infections.[46] In South America *T. cruzi* is very prevalent in Brazil, Argentina, Chile, Uruguay and Venezuela and to a lesser extent in Bolivia, Colombia, Ecuador, Peru, and French Guiana. In Central America it has been found in Panama, Costa Rica, Mexico, and Guatemala. A few indigenous cases have been diagnosed in man in the Southern United States. Natural infections due to both trypanosomes have also been isolated from a wide range of animals in areas where the infections have been diagnosed in man.

The two trypanosomes can be distinguished by their morphology, their site of development in the vector, their mode of infection and also their effects on man.

T. cruzi

Trypanosomiasis due to *T. cruzi* is more common in children than in adults. The disease is most prevalent in rural areas and in the poor classes who live in thatched huts where the walls offer excellent hiding places for the insect vector. Sex and race are unimportant.

(i) *Natural infections.* The importance of wild animals as reservoirs is well known and over 100 species and subspecies of wild animals have been found infected.[9,17] In this section we are mainly concerned with some of the more recent reports which are not covered in two previous reviews (Table II).

Among the wild animals in South America the armadillos and opossums are considered the chief reservoir hosts. This trypanosome has also been reported in monkeys, anteaters, bats, ferrets, foxs, raccoons, squirrels, skunks, rats and mice. In the United States the trypanosome has been only recorded in the southern states. Among the naturally infected wild animals are: opossums, raccoons, grey foxes, striped skunks, wood rats, and antelope squirrels.

In South America, dogs, cats and possibly pigs are considered important domestic reservoirs. In endemic areas 8-31% of the dogs and 8-18% of the cats have been found infected.

(ii) *Experimental infections.* Recent work on experimental infections of wild animals included reports by Petana[44,45] and Porter.[47]

TABLE II. *Reservoir Hosts of* Trypanosoma cruzi

Naturally infected animals	Locality	References
Akodon arviculoides cursor	Brazil	28a
Rattus rattus	Brazil	28b
Nasua narica	British Honduras	38
Didelphis marsupialis	Alabama (U.S.A.)	42b
Didelphis paraguayensis; Rattus rattus frugivorus; R. r. alexandriuus; Zigodontomys pixuna	Brazil	12
Cebus albifrons unicolor; C. apella; Ateles geoffroyi grisescens; A. belzebuth hybridus; Marikina leucopus; Peropteryx m. macrotis; Phyllostoma hastatum; P. discolor; Glassophaga s. sorcina; Carollia p. perspicillata; Artibeus lituratus; Desmodus r. rotundus; Molossus m. major	Colombia	39
Procyon lotor; Nasua narisa bullata	Costa Rica	7
Cavia a. aperea	Brazil	29
Carollia perspicillata; Didelphis marsupialis	Brazil	13
Didelphyis marsupialis anrita	Brazil	11
Phylostomus hastatus; Didelphis marsupialis	Brazil	19
Coendon insidiosus	Brazil	50
Dasyprocta azarae	Brazil	14
Galictis cuja furax	Brazil	30
Callicebus nigrifrons	Brazil	1
Didelphis marsupialis	British Honduras	45
Didelphis marsupialis; Dasypus novemcinctus fenestratus; Conepatus tropicalis trichurus; Philander opossum fuscogriseus; Marmosa alstoni	Costa Rica	59

Feces containing trypanosomes from a wild caught *Triatoma dimidata* produced an infection when inoculated into a male Peteis climbing rat *(Tylomas nudicaudus).*[44] Petana[45] infected 4 species of rats *(Heteromys desmarestianus, Ototylomys philotis, Tylomys nudicaudus,* and *Oryzomys)* and found them all highly susceptible while two others *(Nyctomys sumichrasti* and *Nasua narica)* were more resistant and only scanty intracellular forms were seen. Skunks *(Mephitis mephitis)* and opossums *(Didelphis marsupialis)* have also been infected.[47]

Ryckman[48,49] experimentally infected two lizards *(Gerrhonotus multicarinatus tigris multisculatis)* with *T. cruzi* by injection and by using a vector.

Experimental infections with *T. cruzi* have also been produced in the common laboratory animals (e.g. mice, rats, guinea pigs) and in dogs and cats. In a study on farm animals as possible reservoir hosts in the United States, Diamond and Rubin[21] experimentally infected young pigs, lambs, kids, and calves with a strain isolated from a raccoon in Maryland. The infection persisted for at least 57 days in pigs, 53 to 85 days in lambs, 38 days in a kid, and 21 days in a calf.

T. rangeli

Its known distribution is somewhat more limited than *T. cruzi*, but further studies might prove otherwise. So far it has been recorded in man in Venezuela, Guatemala, Colombia, Chile, El Salvador, and Costa Rica. Since the vector is a reduviid bug, transmission takes place chiefly in the home, and as expected is more prevalent in children.

(i) *Natural Infections.* In rural areas cebus monkeys, opossums and anteaters are considered the chief reservoir hosts (Table III) while in urban areas dogs are the most commonly infected domestic animals.

(ii) *Experimental infections.* Young mice and rats are quite susceptible to infection. Monkeys and opossums can be infected.[33,41]

TABLE III. *Reservoirs of* Trypanosoma rangeli

Naturally infected animals	Locality	References
Didelphis m. marsupialis	Brazil	16
Metachirops o. opossum	Brazil	16
Marmosa a alstoni; Philander opossum fuscogrisens; Didelphis marsupialis	Costa Rica	40
Didelphis marsupialis; Philander opossum	Brazil	17, 18
Saimiri boliviensis	Peru	42
Cebus capucinus; Glossophago S. saorcina; Artibeus lituratus	Colombia	39
Tamandua tetradactyla	Panama	54

Discussion

Since both African and American trypanosomes which infect man lack specificity in their choice of vertebrate hosts, animal reservoirs may play an important role in the epidemiology of human trypanosomiasis. Although nearly all domestic animals and a large group of wild animals can be infected experimentally with African trypanosomes, isolation of human trypanosomes from animals has been reported in only a few cases. This is due to the fact that at present human volunteers have to be used for differentiating *T. brucei* from *T. gambiense* and *T. rhodesiense* if the isolation is made from animals. The evidence of animal reservoirs of *T. gambiense* and *T. rhodesiense* will remain meagre until some better methods of differentiation of *T. brucei* group are found. However, experimental infection of wild and domestic animals with *T. rhodesiense* suggests that these animals could be potential reservoirs. The evidence of natural and experimental infection with *T. cruzi* in large numbers of domestic and wild animals indicate that these animals form important reservoirs for Chagas disease.

Both African and American trypanosomiasis of man occur mainly in rural areas, where the vectors are usually more abundant. In African trypanosomiasis infection usually takes place in the bush, while in American trypanosomiasis man becomes infected at home infested with reduviid bugs.

Since tsetse flies live far from the human community domestic animals particularly dogs and cats infected with *T. rhodesiense* or *T. gambiense* do not present the same danger as animals infected with *T. cruzi*. The role of dogs and cats in the epidemiology of Chagas disease is twofold; (1) acting as reservoir for the strain acquired from man (2) bringing into a human population a strain acquired from wild animals through the bites of infected insect vectors near or in the nest of wild rodents and also by eating infected animals such as rats.

Since it is generally accepted that the vector is mainly responsible for the introduction of the infection into a community, the possible role played by dogs and cats has often been overlooked.

Lacking any effective chemoprophylactic or immunizing agents, insecticides provide one of the most effective control methods for the vectors of Chagas disease.

In African trypanosomiasis manipulation of environment by selective clearing of vegetation which forms a favourable habitat of tsetse flies, the use of insecticides and chemotherapeutic drugs constitute the present control methods.

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