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The coati (*Nasua nasua*, Carnivora, Procyonidae) as a reservoir host for the main lineages of *Trypanosoma cruzi* in the Pantanal region, Brazil

H.M. Herrera[a,b], **C.V. Lisboa**[a], **A.P. Pinho**[a], **N. Olifiers**[c,d], **R.C. Bianchi**[b], **F.L. Rocha**[b], **G.M. Mourão**[b], **A.M. Jansen**[a,*]

[a] *Laboratório de Biologia de Tripanosomatídeos, Instituto Oswaldo Cruz/FIOCRUZ, Av. Brasil 4365, Rio de Janeiro, RJ, 21040-900, Brazil*
[b] *Laboratório de Fauna Silvestre, Centro de Pesquisa Agropecuária do Pantanal, Embrapa/Pantanal, Rua 21 de Setembro, 1880, Corumbá, MS, 79320-900, Brazil*
[c] *Department of Fisheries and Wildlife Sciences, University of Missouri, Columbia, MO 652110-740, USA*
[d] *Laboratório de Biologia e Parasitologia de Mamíferos Silvestres Reservatórios, Instituto Oswaldo Cruz/FIOCRUZ, Av Brasil 4365, Rio de Janeiro, RJ, 21040-900, Brazil*

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Summary We have focused on the role played by a carnivore, the coati (*Nasua nasua*), in the transmission cycle of *Trypanosoma cruzi* in the Brazilian Pantanal biome. We collected data during 2000/01 and 2005—07. Prevalence and pattern of *T. cruzi* infection were determined by serological tests and hemoculture. Isolates were characterized by miniexon molecular assay. Our results demonstrate that *T. cruzi* transmission cycle among coatis in the southern Pantanal seems to be well established, as we found high serum prevalences and high parasitemias throughout the two studied periods. Single infections by TCII (32.1%), TCI (28.0%) and Z3 (7.1%) were observed. Mixed infections by TCI/TCII (10.7%) and TCI/Z3 (3.6%) were also detected. Distinct genotypes of *T. cruzi* could be recovered during the 8 months follow-up of the same animals. As free-living coatis have high densities and inhabit all habitats, they may play an important role in the maintenance and dispersion of the main *T. cruzi* subpopulations. Considering that the Pantanal connects some of the major biomes of South America, it may be acting as a corridor for the spread of the main *T. cruzi* subpopulations. Our data give support that predator—prey links are important mechanisms for *T. cruzi* transmission and perpetuation in the wild.

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* Corresponding author. Tel.: +55 21 25984324; fax: +55 21 25606572.
E-mail address: jansen@ioc.fiocruz.br (A.M. Jansen)..

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1. Introduction

Trypanosoma cruzi, the etiological agent of Chagas disease, is a highly adaptable and successful protozoan parasite and is able to colonize almost every tissue of its multiple mammalian hosts. The biological flexibility of this trypanosomatid is probably the result of a long evolutionary process undergone by numerous clones in its mammalian hosts, in their distinct biomes and habitats. As well as infection with metacyclic forms voided in the feces of infected triatomine bugs, other dispersal strategies are also noticeable, as *T. cruzi* may be naturally transmitted via the oral route and congenitally. The oral route is probably the most ancient and main route of this parasite in the wild. Moreover, the recent outbreaks of human disease due to ingestion of contaminated food and beverages with *T. cruzi* insect-derived metacyclic trypomastigotes have also emphasized the importance of oral transmission in human infection (Steindel et al., 2008). Indeed, the enhancement of trypomastigote infectivity in the acidic environment of the stomach has already been described (Yoshida, 2006).

As a primarily zoonotic infection, *T. cruzi* displays a complex epidemiological scenario that includes more than 100 species of mammalian hosts, several dozens of Triatominae (vectors) and different parasite subpopulations. Furthermore, *T. cruzi* enzootiology shows regional and temporal particularities, as well as ecological macro- and micropeculiarities that interfere in the relationships among its mammalian host species (Lisboa et al., 2004; Xavier et al., 2007).

Although described as a single species, *T. cruzi* includes two main distinct phylogenetic groups (lineages), as recognized following an international agreement (Satellite Meeting, 1999). The geographic distribution of these lineages and a putative correlation with hosts and human disease are far from being clear. Undoubtedly, the sublineage *T. cruzi* I (TCI) circulates in extensive areas of almost all American biomes (Cortez et al., 2006; Coura et al., 2002; Samudio et al., 2007). The infection by this genotype has been described in a broad range of wild mammalian species, and perhaps this aspect has led to the association of TCI with the sylvatic transmission cycle. By contrast, the subpopulation of *T. cruzi* II (TCII) is associated with intradomiciliar transmission and domestic and peri-domestic mammalian species (Miles et al., 1981; Yabsley and Noblet, 2002; Yeo et al., 2005). It has been demonstrated that TCII may circulate sympatrically with TCI in the same sylvatic area, according to habitats, fauna composition and social, cultural and economic characteristics, infecting free-ranging mammals from several orders throughout the Neotropical region (Ceballos et al., 2006; Lisboa et al., 2004; Pinho et al., 2000; Rozas et al., 2007; Salazar et al., 2006; Xavier et al., 2007).

The constant use of molecular tools has confirmed that *T. cruzi* is a pleomorphic protozoan (Brisse et al., 2000; de Freitas et al., 2006; Macedo et al., 2004; O'Connor et al., 2007). In this sense, among TCII strains, five discrete genetic subdivisions or discrete typing units (DTUs) (IIa-e) were recognized (Brisse et al., 2000). Even within each of these sublineages there is extensive genetic diversity (Macedo et al., 2004). Also within TCI, high genetic variability has been observed (O'Connor et al., 2007; Salazar et al., 2006).

As well as TCI and TCII, there are a number of *T. cruzi* strains that cannot be properly grouped into any one of these two major lineages, and their definitive taxonomic position is still under debate. By consensus, these strains were included in Miles' zymodeme Z3 (Mendonça et al., 2002; Miles et al., 1981; Pedroso et al., 2007). However, DNA sequencing revealed that some of these isolates have hybrid characteristics, and they were included in *T. cruzi* II subgroups IIa and IIc (Brisse et al., 2000; Sturm et al., 2003). Currently, it has been proposed that a third genotype, TCIII, can bring back together these strains (de Freitas et al., 2006).

Despite the long-standing recognition of *T. cruzi* infection in North and South American carnivores, the details of the pattern of infection and the role of this taxon in the sylvatic transmission cycle remain poorly studied (John and Hoppe, 1986; Lainson, 1965). Procyonids (Mammalia, Carnivora) are first recorded in South America in Late Miocene deposits from Argentina (Berta and Marshall, 1978). Two genera of this family are geographically distributed throughout the Americas: coatis (*Nasua* spp.) and raccoons (*Procyon* spp.). These genera inhabit terrestrial to arboreal ecological niches in different habitats. Moreover, as a result of their diverse diets, procyonids contrast with many other species in the Carnivora. Indeed, coatis feed from three trophic levels, feeding on fruits, invertebrates, eggs and small vertebrates (Nowak, 2005).

We undertook a study on *T. cruzi* infection in *Nasua nasua* in the Pantanal biome, the largest seasonal wetland, which has an extraordinarily abundant wildlife (Lourival and Fonseca, 1997). Our results contribute to the understanding of the role played by this abundant carnivore species in the transmission and maintenance of the main genotypes of *T. cruzi* in the Pantanal region.

2. Materials and methods

2.1. Study area

We collected data in the southern Pantanal biome, a large seasonal floodplain covering about 140 000 km^2 in the core of South America. Although this region is considered a distinct ecosystem, its vegetation (dominated by species of *cerrado* similar to African savannahs) varies in extension and density, forming a mosaic of habitat types (Figure 1): (1) '*cerrado*' — small, twisted or gnarled trees, thinly spaced with herbaceous layers formed by grasses and shrubs; (2) 'grassland' — open grassland fields flooded eventually under great inundation; (3) 'field *cerrado*' — a mix of *cerrado* and grassland; (4) 'forest' — higher ground covered by dense semideciduous forest, free of seasonal flood margined with dense bromeliacea bushes mixed with bushy shrubs and vines; (5) 'lakes' — shallow lake basins, many of them seasonally flooded.

The study area is located 160 km east from Corumbá city, Brazil, between 537028 to 544690 (east) and 7896896 to 7904119 (north) (coordinates Universal Transverse Mercator, UTM, zone 21K), covering about 100 km^2. In this region, weather conditions are markedly seasonal. During the wet season (November—April), many parts of open grassland change from terrestrial habitats into aquatic ones. In the