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REVIEW ARTICLE

The clinico-pathology and mechanisms of trypanosomosis in captive and free-living wild animals: A review

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Abstract Reports on the clinico-pathology and mechanisms of trypanosomosis in free-living and captive wild animals showed that clinical disease and outbreaks occur more commonly among captive than free-living wild animals. This is because the free-living wild animals co-exist with the disease until subjected to captivity. In exceptional cases however, draught, starvation and intercurrent diseases often compromised trypanotolerance leading to overt trypanosomosis in free-living wild animals. Meanwhile, in captivity, space restriction, reduced social interactions, change in social herd structure, reduced specie-to-specie specific behaviors, altered habitat and translocation were the major stressors that precipitated the disease. The cumulative effect of these factors produced severe physiological and somatic stress leading to diminished immune response due to increased blood cortisol output from adrenal cortex. The major symptoms manifested were pyrexia, innapetence, increased respiration, anaemia, cachexia and death. At necropsy, pulmonary oedema, splenomegally, hepatomegally, lympadenopathy and atrophy of body fats were the gross changes encountered. At the ultra-structural level, the tissues manifested degenerative changes, haemorghages, necrosis and mononuclear cellular infiltrations. The mechanisms of cellular and tissue injuries were primarily associated with physical and metabolic activities of the organisms. From the foregoing, it is evident that stress is the underlying mechanism that compromises trypanotolerance in wild animals leading to severe clinico-pathological effects.

Keywords Captive wild animals · Clinico-pathology · Free-living wild animals · Trypanosomosis

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Introduction

Trypanotolerance in wild animals is the relative capacity to control the development of the parasites and to limit their clinico-pathalogical effects (d' Iteren et al. 1998). Because of this innate ability, they act as reservoir hosts to pathogenic African trypanosomes such as *Trypanosoma vivax*, *T. brucei*, *T. congolense*, *T. equiperdum*, *T. b. gambiense* and *T. cruzi* (Ashcroft 1959; Baker 1968; Averbeck et al. 1991). These species of trypanosomes have however produced clinical disease in free-living wild animals (Evans 1910; Adams and Lionnet 1933; Baker 1968), captivity (Parija and Bhattacharya 2005; Mbaya et al. 2008a) and under experimental conditions (Mihok et al. 1991; Abenga and Anosa 2006; Mbaya et al. 2008b, c, d, e).

In tsetse-infested areas, several *Glossina* species are the main arthropod vectors while other haematophagus biting flies facilitate mechanical transmission especially in tsetse- free areas of the world (Mbaya et al. 2008a). In addition to these methods of transmission, oral transmission to predatory carnivores via abrasions in the oral mucosae, caused by bone splinters of infected prey have been reported (Baker 1968) and demonstrated experimentally in bush babies (*Galago crassicaudatus*) (Duke et al. 1934; Heisch 1963).

The clinico-pathology of trypanosomosis vary in intensity from the mild form usually seen in free-living wild animals (Evans 1910; McCulloch 1967; Adamson 1965) to the often fatal type culminating in outbreaks among captive wild animals (Parija and Bhattacharya 2005, Mbaya et al. 2008a). The low intensity of the infection among free-living wild animals that tend to co-exist with the infection is due to the reduced stress the animals encounter in their natural ecosystem (Grootenhuis 1987). This may however, be compromised in the event of starvation, draught, intercurrent infections, translocation and captivity (IUCN 1998; Mbaya 2007). In spite of the relative importance of the subject as it relates to *in-situ* and *ex-situ* conservation of wild animals, information on the trypanosomosis of captive and wild animals is fragmentary. This review was therefore, carried out to investigate and document the clinico-pathology of trypanosomosis and the mechanisms of the disease in free-living and captive wild animals.

Prevalence of trypanosomosis in wild animals

The prevalence of trypanosomosis among several captive and free-living wild animals has been reported (Baker 1968; Marie 1998; Reichard 2002; Parija and Bhattacharya 2005; Mbaya 2007; Mbaya et al. 2008a). In East Africa, for instance, trypanosomes were detected in 6.3% of 1,242 game animals of various species including the waterbuck (*Kobus* deffassa) 33%, reedbuck (*Redunca redunca*) 25%, giraffe (*Giraffa camelopardalis*) 16% and 12% in warthogs (*Phacochoerus aithiopicus*) (Ashcroft 1959; Geigy et al. 1967; Tarimo et al. 1991).

In the Serengeti National Park, trypanosomes were present in 28% of 113 lions (*Panthera leo*) but absent in the cheetahs (*Acinonyx jubatus*). A significant variation in the prevalence of trypanosome infections in the four Serengeti habitats sampled was observed with the prevalence being highest in lions (*Panthera leo*) from the Serengeti woodlands, a habitat where tsetse flies are common (Averbeck et al. 1991). Stevens et al. (1989) reported a prevalence of 27% due to *T. evansi* among free-living capybaras (*Hydrochaeris hydrochaeris*) and 58% among semi-captive ones in the Pantanal region of Brazil.

In the tsetse-free arid region of northeastern Nigeria, Mbaya et al. (2008b) observed that captive stripped hyeanas (*Hyeana hyeana*) and spotted hyeana (*Crocuta crocuta*) had

prevalence of 16.7% due to *T. brucei* and 50% due to *T. vivax*. They also reported a prevalence of 50% due to *T. vivax* in Grimm's duickers (*Sylvicaprea grimmia*) and 50% due to *T. vivax* in western kobs (*Kobus kob*). Furthermore, dorcas gazelles (*Gazella dorcas*) had 10% *T. congolense* and 20% *T. vivax* infections while sitatungas (*Tragelaphus speikei*) had 16.6% *T. vivax*, and 33.3%) due to *T. congolense*. Similarly, red fronted gazelle (*Gazella rufifrons*) had 50% and 7.1% infections due to *T. brucei* and *T. congolense* respectively. Dunn et al. (1963) examined 223 Peruvian and Columbian monkeys and marmosets (*Callithrix pennicillata*) and reported a prevalence of 21% for *T. cruzi*.

Reservoir status of wild animals

The innate ability of wild animals to co-exist with trypanosomes without suffering overt disease constitutes their reservoir status. Several studies have shown that certain wild ungulates serve as reservoirs of pathogenic African trypanosomes of livestock (Baker et al. 1967; MMH 1987; Connor 1994; Lovemore 1994; Marie 1998; Reichard 2002) while primates and antelopes were identified as potential reservoirs of human trypanosomes such as *T. brucei gambiense* and *T. brucei rhodesiense* (Kaguraka 1992) (Table 1). Early records of natural infections of trypanosomes in wild animals included the finding of *T. evansi* in Indian elephants (*Elaphus maximus*) (Evans 1910) and sambar deer (*Cervus unicolor*) (Adams and Lionnet 1933) and *T. equinum* in capybaras (*Hydrochaeris hydrochaeris*) (Migone 1910). In Lengwe National Park and M'gele Game Reserves in Central Africa, the nyala (*Tragelaphus angassi*) was the main reservoir host to several pathogenic African trypanosomes (Nyasulu and Pugh 1987). In South America, Shaw and Lianson (1972) reported the reservoir status of the Venezuelan deer (*Odocoilus virginianus gymnotis*) for *T. vivax*. Similarly, in South America, apparently healthy capybaras (*Hydrochaeris hydrochaeris*) (Morals et al. 1976), ocelot (*Felis pardalis*) and the vampire bat (*Desmodus rotandus*) (Hoare 1965; Shaw 1977) served as reservoirs of *T. evansi* where the later played an important role in initiating outbreaks of surra later sustained by haematophagus flies (Constantine 1970).

A summary of reports of trypanosome species in various captive wild animal species is presented in Table 2. The capybaras (*Hydrochaeris hydrochaeris*), (Stevens et al. 1989; Nunes et al. 1993), red fronted gazelles (*Gazella rufifrons*) in Abuja and Maiduguri zoos (Mbaya 2007), white tigers (*Panthera tigris*) and Bengal tigers (*Panthera tigris*) in Nandankanan zoo (Parija and Bhattacharya 2005) were severely infected with *T. evansi*. Meanwhile, a lion (*Panthera leo*) (Barnett 1989) and spotted hyeana (*Crocuta crocuta*) (Baker 1968) were infected with *T. brucei* in London zoo.

In the tsetse free semi-arid region of north-eastern Nigeria, however, captive stripped hyeana (*Hyeana hyeana*), spotted hyeana (*Crocuta crocuta*), Grimm's duicker (*Sylicaprea grimmia*), western kob (*Kobus kob*), dorcas gazelle (*Gazella dorcas*), red fronted gazelles (*Gazella rufifrons*) and sitatunga (*Tragelaphus speikei*) were identified as potential reservoirs of various species of pathogenic trypanosomes of livestock (Mbaya et al. 2008a).

Clinical signs and mechanisms of trypanosomosis in wild animals

Clinical trypanosomosis has been reported to occur more commonly among captive than free-living wild animals (Parija and Bhattacharya 2005; Mbaya et al. 2008a). This is because, many cases of presumed resistance to trypanosomosis frequently break down

Table 1 Summary of reports of various trypanosome species encountered among free-living wild animals

Geographic locations	Free-living wild animal Species	Trypanosome species	References
Kenya	Waterbucks (*Kobus deffasa*)	*T. brucei*	Ashcroft (1959),
	Reedbucks (*Redunca redunca*)	*T. brucei*	
	Giraffes (*Giraffa camelopardalis*)	*T. brucei*	Geigy et al. (1967)
	Warthog (*Phacochoerus aeithiopicus*)	*T. brucei*	
Serengeti, Tanzania	Elands (*Tauratragus oryx*)	*T. congolense, T. vivax*	Baker (1968)
	Giraffes (*Giraffa camelopardalis*)	*T. vivax*	"
	Grant's gazelles (*Gazella granti*)	*T. congolense*	"
	Hartebeests (*Alcelaphus buselaphus*)	*T. brucei, T. vivax*	"
	Cape hunting dogs (*Lyean pictus*)	*T. congolense*	"
	Spotted hyeanas (*Crocuta crocuta*)	*T. congolense*	"
	Impalas (*Aepyceros melampus*)	*T. brucei*	"
	Reedbucks (*Redunca redunca*)	*T. brucei*	"
	Lion (*Panthera leo*)	*T. brucei*	"
	Thompson's gazelles (*Gazella thompsoni*)	*T. congolense*	"
	Topi (*Damaliscus korrigum*)	*T. brucei, T. vivax,*	"
	Warthog (*Phacochoerus aeithiopicus*)	*T. congolense*	"
	Waterbucks (*Kobus deffasa*)	*T. brucei, T. congolense*	"
	Wildebeests (*Connochates taurinus*)	*T. congolense*	"
	Zebra (*Equus burchelli*)	*T. brucei, T. congolense*	"
	Lions (*Panthera leo*)	*T. brucei, T. congolense*	Averbeck et al. (1991)
Pantanal, Brazil	Capybaras (*Hydrochaeris hydrochaeris*)	*T. equinum*	Migone (1910).
		T. evansi	Stevens et al. (1989).
Lengwe Park, Malawi	Nyala (*Tragelaphus angassi*)	Unspecified	Nyasulu and Pugh (1987)
Malawi	Buffalos (*Syncerus caffer*)	Unspecified	Malawi, Ministry of Health
	Waterbucks (*Kobus deffasa*)	Unspecified	
	Reedbucks (*Redunca redunca*)	Unspecified	
	Bushbucks (*Tragelaphus scriptus*)	Unspecified	
	Kudu (*Tragelaphus streptisceros*)	Unspecified	
Sambisa National Park, Nigeria	Red fronted gazelles (*Gazella rufifrons*)	*T. brucei*, *T. vivax*	Mbaya (2007)
	Dorcas gazelles (*Gazella dorcas*)	*T. vivax, T. congolense*	
Ngulia Rhino Sanctuary, Tsavo	Rhinoceros (*Diceros bicornis*)	*T. congolense*	Mihok et al. (1992)
South America	Ocelots (*Felis pardalis*)	*T. evansi*	Hoare (1965).
	Vampire bats (*Desmodus rotandus*)	*T. evansi*	Shaw (1977).
	Venezuelan deer (*Odocoilus virginianus gymnotis*)	*T. vivax*	Shaw and Lianson (1972).

Table 1 (continued)

Geographic locations	Free-living wild animal Species	Trypanosome species	References
	Capybaras (*Hydrochaeris hydrochaeris*)	*T. evansi*	Morals et al. (1976).
New Mexico	Armadillos (*Dasypusnovem cinatus*)	*T. cruzi*	Wood and Wood (1941), (1961)
	Racoons (*Procyon lotor*)	*T. cruzi*	
	Foxes (*Urocyon cinercorgenteus*)	*T. cruzi*	
	Opossums (*Dilelphis marsupialis*)		"
Peruvia/Columbia	Marmosets (*Callithrix penicillata*)	*T. cruzi, T. minassense*	Dunn et al. (1963).
	Peruvian squirrel monkeys (*Scimiri boliviensis*)	*T. rangeli*	
India	Indian elephant (*Elaphus maximus*)	*T. evansi*	Evans (1910).
	Sambar deer (*Cervus unicolour*)	*T. evansi*	Adams and Lionnet (1933).

when free-living wild animals are translocated from their natural habitat and subjected to the stress of captivity (Marie 1998; Reichard 2002; Parija and Bhattacharya 2005).

The pathophysiologies of stress in captivity often trigger the secretion of increased levels of adrenocorticotrophic hormone (ACTH) via hypothalamic influence. This in turn stimulates the adrenal gland to secrete excess corticosteroid leading to immunossuppression in wild animals (Boere et al. 2005; Mbaya et al. 2008b). Excessive stimulation and activity of the adrenal gland with increased cortisolaemia occurred in red fronted gazelles (*Gazella rufifrons*) experimentally infected with *T. brucei* (Mbaya 2007; Mbaya et al. 2008b). This mechanism was the principal factor responsible for the break down of trypanotolerance in the gazelles subjected to captivity for the first time (Mbaya 2007; Mbaya et al. 2008b). This factor might explain why translocation of wild mammals from one region to another for the reinforcement of captive breeding or exhibition frequently result in the outbreaks of overwhelming cases of trypanosomosis (IUCN 1998).

Translocation of wild animals from their natural habitat to captivity often results in the importation of pathogenic species of trypanosomes, which can adversely affect the managed species (either the translocated wild animal or the captive resident animals of the same species, other captive resident species at the translocation site or both). This may be partly, responsible for the death of the lioness called 'Elsa' that died of cardiac related symptoms associated with *T. congolense* infection while in captivity in the London zoo (Barnett 1989). Similarly, Baker (1968) reported a case of trypanosomosis due to *T. brucei* infection in a captive female rhinoceros (*Bicornis bicornis*) in the London zoo where the clinical signs observed were inappetence, lethargy, lacrimation and pyrexia. Most conservationists believe that environmental enrichment with the provision of conditions close to situations in the wild could prevent the breakdown of innate resistance and allow free-living wild animals thrive in captivity. However, a spotted hyeana (*Crocuta crocuta*) translocated from Uganda to the London zoo eventually manifested symptoms of trypanosomosis due to *T. brucei* (Barnett 1989).

Nunes et al. (1993) demonstrated the presernce of *T. evansi* in the peripheral blood of free-living coatis (*Nasua nasua*) and capybaras (*Hydrochaeris hydrochaeris*) translocated to captivity. The wild dogs manifested various degree of lassitude while in captivity in Brazil.

Table 2 Summary of reports of various trypanosome species encountered among captive wild animals

Geographic locations	Captive wild animal species	Trypanosome species	References
Pantanal zoo, Brazil	Capybaras (*Hydrochaeris hydrochaeris*)	*T. evansi*	Stevens et al. (1989), Nunes et al. (1993).
	Coatis (*Nasua nasua*)	*T. evansi*	Nunes et al. (1993).
Nandankanan Zoo, India	White tigers (*Panthera tigris*)	*T. evansi*	Parija and Bhattacharya (2005)
	Bengal tigers (*Panthera tigris tigris*)	*T. evansi*	
London, Zoo	Lion (*Panthera leo*)	*T. congolense*	Barnett (1989).
	Spotted hyena (*Crocuta crocuta*)	*T. brucei*	Baker (1968).
	Rhinoceros (*Bicornis bicornis*)	*T. congolense*	"
	Zebra (*Equus burchelii*)	*T. evansi*	"
Abuja, Zoo, Nigeria	Wildebeest (*Connochaetes taurinus*)	*T. evansi*	Mbaya (2007)
	Red fronted gazelles (*Gazella rufufrons*)	*T. brucei*	"
Sanda Kyarimi, Zoo, Nigeria	Stripped hyeanas (*Hyeana hyeana*)	*T. brucei*	Mbaya et al. (2008a)
	Spotted hyeanas (*Crocuta crocuta*)	*T. vivax*	"
	Grimm's duickers (*Sylvicaprea grimmia*)	*T. vivax*	"
	Western kobs (*Kobus kob*)	*T. vivax*	"
	Dorcas gazelles (*Gazella dorcas*)	*T. congolense*	"
	Sitatunga (*Tragelaphus speikei*)	*T. vivax, T. congolense*	"
	Red fronted gazelles (*Gazella rufifrons*)	*T. brucei*	"

An outbreak of trypanosomosis occurred among white tigers (*Panthera tigris*) and Bengal tigers (*Panthera tigris tigris*) at the Nandankanan zoo in India (Parija and Bhattacharya 2005). According to conservation biologists, this is the largest incident of disease related deaths of tigers in captivity worldwide. The clinical signs observed were intermittent fever, anaemia and progressive weight loss. Outbreaks of trypanosomosis due to *T. brucei* with clinical signs of pyrexia, anaemia and death were also observed and reported among captive red fronted gazelles (*Gazella rufifrons*) in zoological gardens in Maiduguri and Abuja, Nigeria (Mbaya 2007).

Experimental infections in wild animals

Contrary to the view that wild animals are refractory to trypanosomosis, experimental infections reveal wide possibilities (Table 3). Many of these experimental infections produced severe clinical disease (Duke *et. al*. 1934; Heisch 1963; Baker 1968; Grootenhuis *et. al*. 1990; Mihok et al. 1991; Abenga and Anosa 2006; Mbaya 2007; Mbaya et al. 2008b, c, d, e) while some were refractory (Olubayo 1992; Olubayo and Brunn 1992; Olubayo *et. al*. 1990; 1991). Earlier accounts were described for *T. evansi* in *Cervidae* (deer), *Cercopithecidae*) (old world monkeys) and *Sciuridae* (Squirrels) (Packchanian 1938; Kraneveld and Mansjoer 1952) and *T. equinum* in *Didelphis azarae* (opossum) and *Pseudolopex* (fox) (Fornari et al. 1964).

Furthermore, Mesnil and Rouget (1907) and Packchanian (1963) experimentally infected old world monkeys (*Cercopithecidae*) with *T. equiperdum*. However, in a comparative study between the waterbuck (*Kobus deffasa*) and the Boran cattle (*Bos indicus*),

Table 3 Summary of reports of various wild animal species experimentally infected with trypanosomes

Wild animal species experimentally infected	Specie/strain of trypanosomes	Route of infection	References
Bush babies (*Galago crassicaudatus*)	*T. brucei rhodesiense*	Orally	Duke et al. (1934), Heisch (1963).
Rhesus monkeys (*Macaca mulatta*)	*T. cruzi*	Intravenously	Baker (1968).
Common vole (*Microtus arvalis*)	*T. equiperdum*	Intraperitoneally	Horváth et al. (1987).
Waterbuck (*Kobus deffasa*)	*T. congolense* (IL- 2895)	Via- tsetse fly	Mihok et al. (1991).
African buffalo (*Syncerus caffer*)	*T. congolense*	Via- tsetse fly	Grootenhuis et al. (1990).
Waterbuck (*Kobus deffasa*)	*T. congolense* (IL-2895)	Intravenously	Olubayo et al. (1991), Olubayo (1992).
African buffalo (*Syncerus caffer*)	*T. congolense* (IL-2895)	Intravenously	Olubayo et al. (1990), Olubayo and Brunn (1992), Olubayo and Brunn (1992).
Black rhinoceros (*Diceros bicornis*)	*T. congolense*	Via-tsetse fly	Mihok et al. (1992).
Baboons (*Papio anubis*)	*T. brucei gambiense* (NITR/Abraka)	Intravenously	Mbaya et al. (2009).
Vervet monkeys (*Cercopethicus aethiops pygerythrus*)	*T. brucei gambiense* (NITR/Abraka)	Intravenously	Abenga and Anosa, (2006).
Red fronted gazelles (*Gazella rufifrons*)	*T. brucei* (Mkar/84/NITR/6)	Intravenously	Mbaya (2007), Mbaya et al. (2008b), (c), (d), (e)
Sambar deers (*Cervus unicolor*).	*T. evansi*	Intravenously	Packchanian (1938), Kraneveld and Mansjoer (1952).
American deer mice (*Peromyscus maniculatus*)	*T. hippicum, T. equiperdum*	Intraperitonealy	Packchanian (1963).
	T. brucei	Intraperitonealy	Anosa and Kaneko (1984).
Opossums (*Dilephis azarae*)	*T. equinum*	Intraperitonealy	Fornari et al. (1964).
Foxes (*Pseudolepex* specie)	*T. equinum*	Intravenously	Mesnil and Rouget (1907).
Old world monkeys (*Cercopethitedidae* specie)	*T. equiperdum*	Intravenously	Packchanian (1963).

experimental infection with *T. congolense* clone IL-2895 could not establish initially except following the development of the parasite in tsetse fly (Mihok et al. 1991). Similarly, five waterbucks (*Kobus deffasa*) and four Boran cattle (*Bos indicus*) were infected with the same *T. congolense* strain but using *Glossina morsitans morsitans*. All the cattle became severely anaemic and had to be treated with trypanocides to prevent death. In contrast, tsetse and intravenous challenge of waterbuck (*Kobus deffasa*) resulted in a long pre-patent period followed by brief, intermittent low levels of parasitaemia and eventual self-cure (Olubayo et al. 1991). Self-cure is the ability of an animal to rid itself of infection following secondary challenge. The waterbuck (*Kobus deffasa*) did not become anaemic, even during the short bouts of very low parasitaemia. The waterbucks (*Kobus deffasa*) developed parasite-specific antibodies while the cattle failed to do so (Mihok et al. 1991; Olubayo et al. 1991). The authors concluded that the ability of the waterbuck (*Kobus deffasa*) to resist trypanosome infections was mediated entirely by antibody-dependent immune responses.

On the other hand, red fronted gazelles (*Gazella rufifrons*) experimentally infected with *T. brucei* alone (Mbaya 2007) or concurrently with *Haemonchus contortus* (Mbaya et al. 2008c, e) developed severe clinical disease. The gazelles came down heavily with the infection with parasitaemia rising to as high as 500×10^3/ul during the first and second waves followed by pyrexia well above 43°C.

In contrast to the waterbuck (*Kobus deffasa*) that are completely wild, the red fronted gazelle (*Gazella rufifrons*) that are semi-domesticated may have species characteristics to show high parasitaemia (Mbaya 2007). The undulating temperature in the red fronted gazelle (*Gazella rufifrons*) produced various degrees of testicular degeneration, calcification, atrophy and sclerosis with concomitant aspermatogenesis in males (Mbaya 2007) and abortion in female buffalos (*Syncerus caffer*, Ogaa 1983).

It was also observed that red fronted gazelles (*Gazella rufifrons*) concurrently infected with *T. brucei* and *H. contortus* had shorter pre-patent periods (4 days) and virulent course of infection as against longer periods (8 days) and mild course following infection with *T. brucei* alone (Mbaya et al. 2008c). Similarly, a virulent course of *T. b. gambiense* infection differing from the typically chronic nature of the disease in man was observed in vervet monkeys (*Cercopethicus aethiops pygerythrus*) (Abenga and Anosa 2006) and baboons (*Papio anubis*) (Mbaya et al. 2009).

The effect of the *T. brucei gambiense* infection in the primates caused a major disruption of the circadian rythmicity of sleep and wakefulness, characterized by nocturnal insomnia and diurnal hypersomnia (somnolence) (Abenga and Anosa 2006; Mbaya et al. 2009). In addition, a Peru strain of *T. cruzi* successfully produced typical Ramona's symptom in a rhesus monkey (*Macaca mulatta*), which later exhibited self-cure (Baker 1968). Report on the use of wild rodents in experimental trypanosomosis is scanty. However, the American deer mice (*Peromyscus maniculatus*) have been infected with *Trypanosoma hippicum* and *T. equiperdum* Packchanian (1963) and with *T. brucei* (Anosa and Kaneko 1984). Similarly, Horváth et al. (1987) experimentally infected the common vole (*Microtus arvalis*) with *T. equiperdum*.

Transmission of trypanosomes in wild animals

Mechanical and oral transmission

Mechanical transmission through the painful bite of hamatophagus arthropod vectors of the family *Hypoboscidae*, *Stomoxynae* and *Tabanidae* is one of the methods responsible for the spread of trypanosomosis in tsetse-free and occasionally in tsetse infested areas (Weitz 1963; Baker 1968; Leeflang et al. 1978; Mbaya et al. 2008a). Although, these biting flies other than the tsetse do not remain infected for more than a few minutes during interrupted feedings, their role in the transmission of trypanosomosis is by no means small. Exclusively such biting flies (Weitz 1963; Baker 1968; Leeflang et al. 1978; Mbaya et al. 2008a) spread trypanosomosis in tsetse free zones of Africa, Asia and America. The peculiarity of the mouthparts and the associated painful bite of the mechanical arthropod vectors irritate the host, which immediately ward them off favouring interrupted feedings.

The high prevalence of trypanosomosis among wild carnivores and herbivores not commonly fed on by tsetse flies (*Glossina*) occurring in or near the Serengeti National Park in East Africa was mainly ascribed to mechanical transmissions through the bites of other haematophagus flies (Baker 1960; Adamson 1965; Baker 1968). A similar mode of transmission is responsible for the spread of trypanosomosis among captive wild animals in

the tsetse free arid region of northeastern Nigeria (Mbaya et al. 2008a). The significance of these, concerning transmission, is two-fold. Firstly, the high proportion of infected species of wild herbivores not usually fed on by tsetse, suggests a high level of non-cyclical transmission by other haematophagus mechanical arthropod vectors in such areas (Weitz 1963; Baker 1968; Leeflang et al. 1978). The density of game animal populations in game reserves would doubtless facilitate mechanical transmission by haematophagus flies, by making it easier for a disturbed fly to alight on another host within a sufficiently short time for its proboscis to retain the blood (and possibly trypanosomes) of its previous host (CAB 1989).

Secondly, the remarkably high incidence of trypanosomosis among carnivores, over 80% of the lions (*Panthera leo*) examined at the Serengeti National Park, strongly suggest that these animals, which were rarely fed on by tsetse flies, probably got infected by preying on infected wild herbivores (Baker 1968).

The possibility of oral transmission occurring naturally was demonstrated (Adamson 1965; Baker 1968). Duke et al. (1934) and later Heisch (1963) who successfully experimentally infected bush babies (*Galago crassicandatus*) with *T. brucei rhodesiense* by allowing them to kill and eat an infected laboratory rat reviewed early observations. It is probable in such instances that trypanosomes penetrated small abrasions in the buccal mucosae caused by the bone splinters of the prey (Baker 1968). Successful infection by this means would presumably depend on the predators eating the prey soon after the kill. 'Carrion' feeding might however be less likely to become infective in this fashion (Baker 1968; Mbaya et al. 2008a).

Biological (cyclical) transmission

Biological (cyclical) transmission, involves the development of the trypanosomes in the biological arthropod vector (*Glossina* species). In Pandam Wild life Park located in the Guinea Savannah Zone of Nigeria, biological (cyclical) transmission was responsible for maintaining trypanosomes between wildlife and livestock in the area (Onah et al. (1985). Out of 1029 tsetse flies caught and dissected in Pandam Wild Life Park, Nigeria, 139 (13.5%) were infected with *T. vivax* occurring in 58.7%, 56.8% and 50% of *Glossina palpalis, G. tachenoides* and *G. longipalpalis* respectively. *T. congolense* occurred in 38.1%, 38.6% and 46.1%) while *T. brucei* occurred in 3.2%, 4.6% and 3.1% of the tsetse flies respectively.

The predominant tsetse species associated with the cyclical transmission of trypanosomosis in and around the Serengeti National Park, East Africa, were *Glossina swynertoni* and *G. pallidipes*, with *G. brevipalpalis* being encountered sporadically (Baker 1968; Leeflang et al. 1978). The favoured hosts of the two former species were warthogs (*Phacochoerus aethiopicus*) while *Glossina brevipalpalis* feed mainly on the bushbucks (*Tragelaphus scriptus*) and hippopotami (*Hippopotami amphibius*) (Weitz 1963).

In another study, Sasaki et al. (1995) observed that bushbucks (*Tragelaphus scriptus*) are always in hiding due to their shy disposition and may not be a favoured source of blood meal for *Glossina* while elands (*Tauratragus oryx*) form only 1.4% of the food of *G. swynertoni*. The authors also observed that ostriches (*Struthio camelus*) and African elephants (*Loxodonta africana*) are frequent source of blood meal for *G. pallidipes*. At the Como' National Park in Northern Cote d' Ivoir, out of 1154 blood meal samples examined from *G. tachynoides* 37% were wild ruminants of which, bushbucks (*Tragelaphus scriptus*) represented 57%, hippopotamus (*Hippopotami amphibius*) 19% and the monitor lizard (*Varanus salvadorii*) (19%) (Kupper et al. 1990; Davies-Cole et al. 1994; Torr et al. 1997).

At the Ngulia Rhino Sanctuary, the prevalence of *G. pallidipes* averaged 3.6%, with three times as many *T. vivax* as *T. congolense* infections while *Trypanosoma simiae* and *T. brucei* were present but at low frequency (Mihok et al. 1992). Bugs of the family *Reduviidae* (*Hemiptera*, *Heteroptera*) have a natural transmission cycle for *T. cruzi* to a wide range of wild mammals. These include *Dasypus* (armadillo), *Didelphis* (opossum), *Neotoma* (wood rat), *Procyon* (raccoon), *Pseudolopex* (fox) and *Mustela* (ferret) (Wood and Wood 1941, 1961).

Pathological changes of trypanosomosis in wild animals

Haematological changes

Most researchers believe that anaemia is the major disease-promoting factor in wild animal trypanosomosis (Baker 1968; Ashcroft 1959; Olubayo et al. 1990). Though the reports on free-living wild animals with severe anaemia are scanty, stress associated with starvation, draught, intercurrent infections and translocation often compromised their trypanotolerance leading to severe trypanosomosis (Baker 1968; IUCN 1998). Several authors have reported accounts of anaemia among free-living (Ashcroft 1959; Baker 1968) and captive (Baker 1968; Parija and Bhattacharya 2005; Mbaya 2007) wild animals in several parts of the world.

The degree of anaemia, however, varies with the parasite and host response to the infection. The anaemia is haemolytic in nature as observed in a free-living lion (*Panthera leo*) infected with *T. congolense* and spotted hyenas (*Crocuta crocuta*) infected with *T. brucei* (Baker 1968). Similar observations were encountered in an outbreak of trypanosomosis among captive white tigers (*Panthera tigris*) and Bengal tigers (*Panthera tigris tigris*) (Parija and Bhattacharya 2005).

Experimental infections with *T. brucei gambiense* in vervet monkeys (*Cercopethicus aethiops pygerythrus*) (Abenga and Anosa 2006) and in red fronted gazelles (*Gazella rufifrons*) infected singly with *T. brucei* (Mbaya et al. 2008d) or concurrently with *H. contortus* (Mbaya et al. 2008c, e) also, produced various degrees of haemolytic anaemia. Attempts to however, control anaemia in the African buffalo (*Syncerus caffer*), following experimental infection with *T. congolense* leading to self-cure has been described (Olubayo 1992). This was associated with significant increase of myeloid (CD 11b) cells, which the author believed was responsible for the control of parasitaemia and anaemia. Haemolytic anaemia followed by reticulocytosis was observed in vervet monkeys (*Cercopethicus aethiops pygerythrus*) (Abenga and Anosa 2006) and baboons (*Papio anubis*) (Mbaya et al. 2009) experimentally infected with *T. b. gambiense* while increased erythrocyte sedimentation rate (ESR) was observed following concurrent *T. brucei* and *H. contortus* infections in red fronted gazelles (*Gazella rufifrons*) (Mbaya et al. 2008e). Severe leucopenia, indicating immunosuppression was reported in natural *T. vivax* infection of the Venezuelan deer (*Odocoilus virginianus gymnotis*) (Fiason et al. 1948) and experimentally in a concurrent *T. brucei* and *H. contortus* infection in red fronted gazelles (*Gazella rufifrons*) (Mbaya 2007; Mbaya et al. 2008e). The authors concluded that this mechanism is responsible for the establishment of the infection and the failure of self-cure in these animals.

Gross pathological changes

Per-acute trypanosomosis produced extensive haemorrhages on the serosal surfaces of vital organs in free-living lions (*Panthera leo*), zebras (*Equss burchelli*) (McCulloch 1967),

waterbuck (*Kobus deffassa*), reedbuck (*Redunca redunca*), warthogs (*Phacochoerus aeithiopicus*) (Ashcroft 1959; Geigy et al. 1967), American deer mice (*Peromyscus maniculatus*) (Anosa and Kaneko 1984) and red fronted gazelles (*Gazella rufifrons*) (Mbaya 2007). The authors also observed hepatomegally, splenomomegally, lymphadenopathy and atrophy of body fats.

However, cardiomegally and testicular hypertrophy occurred during the acute phase while shriveling of the heart and testicles were observed during the chronic phase in red fronted gazelles experimentally infected with *T. brucei* (Mbaya 2007; Mbaya et al. 2008c, d and e). Testicular degeneration was reported in buffaloes (*Syncerus caffer*) infected with *T. brucei, T. vivax* and *T. congolense* (Ogaa 1983) while this was coupled with complete depletion of epididymal sperm reserve with complete cessation of spermatogenesis in red fronted gazelles (*Gazella rufifrons*) experimentally infected with *T. brucei* (Mbaya 2007).

Histopathological changes

There is a general paucity of information on histopathological changes in wild animals. This is probably associated with postmortem autolysis, which usually occurred by the time the dead animals are discovered. However, mononuclear cellular infiltration in the central nervous system of a free-living lion (*Panthera leo*) and zebras (*Equus*, *burchelli*) due to *T. brucei* infection in East Africa (McCulloch 1967) was observed. Similar tissue changes occurred in an outbreak of *T. evansi* infection (surra) in the sambar deer (*Cervus unicolor*) in Mauritius (Adams and Lionnet 1933) and in Indian elephants (*Elaphas maximus*) in India (Evans 1910).

In the red fronted gazelle (*Gazella rufifrons*) (Mbaya 2007) and the American deer mice (*Peromyscus maniculatus*) (Anosa and Kaneko 1984), the lesions encountered following an experimental *T. brucei* infection were hyperplasia of the lymphoid nodules and haemosiderosis. The spleen of the red fronted gazelle (*Gazella rufifrons*) in particular, was highly reactive with T-lymphoblastic halos and large numbers of macrophages in the red pulp, while the liver showed widespread periportal hepatocellular necrosis (Mbaya 2007). The lesions in the various tissues and organs were primarily associated with extra vascular localization of *T. brucei*. Erythrophagocytosis and haemosiderosis occurred in all components of the reticulo endothelial system of the sambar deer (*Cervus unicolor*) (Adams and Lionnet 1933), elephants (*Elaphus maximus*) (Evans 1910), American deer mice (*Peromyscus maniculatus*) (Anosa and Kaneko 1984) and red fronted gazelles (*Gazella rufifrons*) Mbaya 2007).

Diagnosis of trypanosomosis in wild animals

Methods such as the wet films, thin smears, lymph node aspirate, and sub-inoculation into susceptible laboratory rodents as well as haematocrit centrifuge technique (HCT) have proved to be effective in the diagnosis of trypanosomosis in wild animals (Onah et al. 1985; Abenga and Anosa 2006; Mbaya et al. 2008a).

The buffy coat dark phase contrast microscopy gave better results among the conventional parasitological techniques in detecting low parasitaemia usually encountered in sub-clinical trypanosomosis in wild animals (Mbaya et al. 2008a). Mbaya (2007) also observed that sub-optimal trypanosomosis in red fronted gazelles (*Gazella rufifrons*) might be detected by certain changes in the levels of total serum proteins, aspartate and alanine amino transferase activity.

Monoclonal antibody assays and Enzyme Linked Immunosorbent Assay (ELISA) antibody capture techniques were sensitive in detecting circulating trypanosome antigens even when the parasites are not detectable in peripheral circulation (Mbaya 2007). Mihok et al. (1991) reported that in order to evaluate the role of the trypanosomes in the Lenge

National Park and Mgete Game Reserve, the Enzyme Linked Immunosorbent Assay (ELISA) and the Card Agglutination Trypanosome Test (CATT) had high specificity. Similarly, the amplification of trypanosome deoxyribonucleic acid (DNA) through Polymerase Chain Reaction (PCR) detected sub-clinical trypanosomosis in apparently healthy wild animals (Mbaya 2007).

Control of trypanosomosis in wild animals

Vector control

The control of trypanosomosis in free-living and captive wild animals involves the control of the biological vectors that transmit the causative agents (Sudarto et al. 1990; Peters 1990; Borrowy et al. 1991; Lavessiere et al. 1991; Bauer et al. 1992). However, the peculiarity of the natural habitat of free-living wild animals makes control difficult since they are not restricted to a particular geographical region (Baker 1968; Barnett 1989).

The behavior of the principal vector (*Glossina*) varies from specie to specie in different localities or even in the same vegetation zone. Therefore, adequate studies on their behavior must precede the actual control effort (Weitz 1963; WHO 1979). In Nigeria, in the past, various control attempts, mainly aimed at eliminating game at the expense of livestock, was unattractive due to conservation and animal welfare issues (Lamorde 1986). Similarly, bush clearing, traps and resettlement of people produced variable successes in Kenya and Uganda (Murray et al. 1990).

Aerosol sprays by helicopters or fixed wing aircrafts along river basins and tsetse habitat have been effective in tsetse control (Johnston et al. 1990) in the past. The main method currently employed to control tsetse flies (Bauer et al. 1992) which was also used decades ago (Dutoit 1954; Jordan 1986), is the use of synthetic pyrethroids to impregnate traps and screens, sometimes additionally baited with odour attractants. The use of special insecticide formulations applied to artificial attractive devices (insecticide-impregnated targets with or without odour attractants) is an efficient and sufficiently specific method to suppress tsetse-target populations in most situations (Challier and Laveissiere 1973; Vale 1974; Brandl 1988; Kupper et al. 1990; SEMG 1995; Bauer et al. 1995; Vale 1998).

Success in tsetse-trypanosomosis control in zoological gardens and game reserves depends largely on a variety of factors. The most important of these are the density and placement of the impregnated attractive devices (Vale 1998). The availability of the attractants for the target tsetse species also plays a vital role (Green 1988; Torr 1994; Torr et al. 1995; Torr et al. 1997). However, the size of the control area, reinvasion pressure and the population dynamics of tsetse populations in adjacent areas must be considered before control can be effective (Vanden Bosshe and Dutchateau 1998; Hargrove et al. 2000).

Bauer et al. (1992) suggested that live targets impregnated with insecticides through spraying, dipping or pour-on treatment are effective in controlling tsetse. One of the major drawbacks of this tsetse fly control technique is that they require the active participation of the majority of communities living within and outside the boundaries of game reserves (Bauer et al. 1992; Jordan 1995).

Chemotherapy/vaccine development

The ability of trypanosomes to change their antigenic coat an infinite number of times makes the development of DNA-vaccine difficult. However, although the development of a

potential vaccine against trypanosomes is possible (Onyeyili and Egwu 1995), chemotherapy remains the only viable option. Diminazene aceturate (Berenil®) at the rate of 7.0 mg/kg body weight was effective in the treatment of experimental *T. brucei* infection in the red fronted gazelle (*Gazella rufifrons*) (Mbaya et al. 2008d). Caution in the use of drugs is, however, required due to drug related toxicity (Jennings 1992).

Similarly, melarsamine hydrochloride (Cymelarsan®) at 0.3 and 0.6 mg/kg body weight was also found to be effective and less toxic in red fronted gazelles (*Gazella rufifrons*) infected with *T. brucei* (Mbaya et al. 2008d) and in an outbreak of trypanosomosis among captive white tigers (*Panthera tigris*) and Bengal tigers (*Panthera tigris tigris*) in Nandankanan zoo, India (Parija and Bhattacharya 2005).

Biological control in wildlife habitat

The technical feasibility of tsetse fly eradication, particularly in wildlife habitats using the sterile insect technique technique (SIT) has been documented (Lindquist et al. 1990; Hendrichs 2000). For maximum effectiveness in wildlife habitats, the sterile males must out number the fertile native males by a considerable margin (Knipling 1995; PAAT 2001) and this may, in certain circumstances, have to be as high as 15 to 1 (PAAT 2001). At the Lake Kariba Wildlife habitat, Zimbabwe, field collected *Glossina morsitans morsitans* adults treated with chemo sterilants and released, caused a drastic decline and subsequent eradication of the tsetse in 26 months. In an earlier experiment in 1988, sterile insects released as pupae, induced 95% sterility in 10 months, however, the experiment could not continue due to civil unrest in the area (PAAT 2001).

In the Tang Wildlife Park, United Republic of Tanzania, following two aerial applications of endosulfan, late-stage *Glossina morsitans morsitans* pupae from goat-fed colony and radiation sterilized with 137C gamma rays, were released into a 195-km^2-control area. The target population of tsetse reduced by 81% and 1 km bush-free barrier zone was however sufficient to prevent reinfestation (PAAT 2001). Similarly, 3,500 Km^2 with 500–600 linear km of riverine forest, an area rich in wild animals initiated in Burkina Faso for the first time in 1981, was sufficient to prevent re-infestation.

Similarly, the Biological Control Project (BICOT) of (1979–1987) in Vom, Nigeria, reared a large number of *G. palpalis palpalis* using guinea pigs, fresh bovine and freeze-dried porcine blood. The colony which consisted of 180, 000 females were released in a ratio of 10:1 in a wildlife habitat of 1,500 Km^2 (with 450 Km of linear riverside forest) with total eradication achieved in 8–12 months. For the first time, sterile virgin females were released and recaptured to confirm the success of the eradication program. However, owing to lack of financial support to extend the eradication area and maintain barriers, reinvasion occurred (PAAT 2001).

Conclusion

In as much as free-living wild animals co-exist with trypanosomosis in their natural habitat, physiological and somatic stress following draught, starvation, intercurrent infections, capture, translocation and captivity often compromised their innate resistance to the infection. Captivity often caused a marked increase in corticosteroid secretion to meet the stressful situation. This is mediated primarily by adrenocorticotrophic hormone (ACTH) through hypothalamic influence, leading to immunossuppression and overwhelming trypanosomosis with severe clinico-pathological effects due to physical and metabolic

activities of the organisms. It is therefore, suggested that stress management by simulating conditions near reality with environmental enrichment, routine screening for trypanosomes, vector control, chemoprophylaxis, and chemotherapy will undoubtedly help in the conservation and propagation of the endangered species.

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