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## The constraining role of disease on the spread of domestic mammals in sub-Saharan Africa: A review

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### ABSTRACT

This paper summarizes and reviews the likely role of infectious diseases as constraints on the spread of domestic animals south of the Sahara. It looks not only at livestock (cattle, sheep, and goats), which have previously received most attention in this regard, but also at dogs, donkeys, and horses. All six species (as well as domestic pigs) originated in Eurasia or North Africa and it is therefore highly likely that on entering the Afrotropical zoogeographic region they will have encountered novel disease challenges to which they were not previously adapted, including pathogens able to 'jump' into them from closely related taxa endemic to sub-Saharan Africa (e.g. Cape buffalo, wildebeest, jackals, zebras). The paper identifies the key diseases involved, considers how arguments for their constraining role can be evaluated further, briefly explores some of the consequences for African history that they have entailed, and emphasizes the importance of also considering the spread of animal diseases that originated with Africa beyond the continent. In particular, it suggests that two important trypanosomal diseases of now global distribution — surra and dourine — may have originally spread out of Africa using donkeys as their principal host.

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### 1. Introduction

The history of food production in sub-Saharan Africa differs from other regions of the Old World in one crucial respect: not one of its more than 100 large mammals was successfully domesticated. While the reasons for this are not completely understood, the consequence is clear: all the mammals kept by people south of the Sahara originated to its north (Gifford-Gonzalez and Hanotte, 2013). Whether entering the Afrotropical (Ethiopian) zoogeographic region (Proches and Ramdhani, 2012) by land or across the Atlantic and Indian Oceans, domestic mammals thus arrived in environments of which they had no prior experience. Once there, they were exposed to novel disease challenges that shaped, constrained, and limited how far they could spread and the directions along which they could expand. These challenges, in turn, helped set the parameters of Africa's history over several thousand years.

Except for trypanosomiasis (e.g. Phillipson, 1982) archaeologists have only recently explored the implications of these diseases. Diane Gifford-Gonzalez's (2000) analysis of the impact of tick-

spread pathogens on the expansion of cattle-keeping in eastern and southern Africa initiated the change. Her principal conclusion, that these diseases (though not necessarily trypanosomiasis, which is not spread by ticks) initially led early herders to prefer sheep and goats over cattle in both regions, has recently been reaffirmed for East Africa, given the continuing absence of evidence for cattle south of Lake Turkana before 3000 BP (Gifford-Gonzalez, 2016). Palaeoenvironmental studies with implications for the prevalence of trypanosomiasis in East and south-central Africa, and thus for the spread of livestock south of the Equator, have also recently appeared (Chritz et al., 2015; Robinson and Rowan, 2017). Other papers have investigated how pathogens may have constrained the expansion of dogs and donkeys, both of which are intrusive to Africa south of the Sahara, even though their close relatives (African wolves, *Canis lupus lupaster*) or immediate ancestors (Nubian wild asses, *Equus africanus africanus*) were present within and north of the modern desert (Mitchell, 2015, 2017b).

The time thus seems right for reviewing our current knowledge of how pathogens affected the expansion of the domestic mammals available to precolonial sub-Saharan societies. In addition, I briefly discuss how we might gain further purchase on the antiquity and geography of the diseases considered, their long-term implications for Africa's human history, and their participation in the web of

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connections linking sub-Saharan Africa to other parts of the world.

## 2. Disease challenges for domestic mammals south of the Sahara

A paper of this length allows discussion of only the most important of the disease challenges encountered by domesticated mammals in sub-Saharan Africa (Table 1). I present them by disease, rather than by victim, since several pathogens affect more than one species, though for ease of reference Table 2 also lists the major disease threats discussed by species. Gifford-Gonzalez and Hanotte (2011, 2013) consider the history of domestic animals in Africa as a whole, complemented by Linseele (2013) for West Africa and Lane (2013) and Gifford-Gonzalez (2016) for East Africa.

### 2.1. Trypanosomiasis

This is among the best known of Africa's insect-borne diseases, not least because its human form (sleeping sickness) affects people. Hosted by over 30 endemic sub-Saharan mammalian taxa, it is caused by parasitic protozoa of the genus *Trypanosoma* that are principally spread by tsetse flies (*Glossina* spp.), although blood-eating (haematophagous) flies and bugs can also act as vectors (Uilenberg, 1998). Three species of *Trypanosoma* primarily infect domestic mammals south of the Sahara. *T. brucei brucei* poses severe dangers to dogs, horses, and donkeys, but is less of a threat to cattle, sheep, and goats. *T. vivax*, on the other hand, produces a relatively mild infection in dogs and equids, but can be severely chronic to acute and quickly fatal in ruminants, while *T. congolense* is most dangerous for them and also commonly fatal to dogs (Auty et al., 2015). Two other taxa (*T. b. gambiense* and *T. b. rhodesiense*) only infect humans (see Fig. 1).

In each case the precise pathogen strain involved and the animal's general health affect the disease's course. In dogs, for example, infection with the more deadly *T. brucei* species augments the effects of any pre-existing infection with *T. congolense* (Lisulo et al., 2014). The picture is made still more complex by variation in the distribution of the different pathogens and by the diversity of *Glossina* species that transmit them. In general terms, however, tsetse flies are found across some 10,000,000 km<sup>2</sup> of Africa between 14°N and 29°S of the Equator wherever suitable shady bush environments exist where they can rest, reproduce, and find non-migratory (usually wild) mammalian hosts. Put broadly, this locates them in areas where mean annual rainfall exceeds 500–700 mm (Nash, 1969).

Several species have evolved a degree of tolerance to trypanosomiasis that allows them to survive, reproduce, and remain productive under trypanosomiasis risk (Yaro et al., 2016). Smaller, humpless, taurine breeds of cattle like the N'Dama, Bambara shorthorn, and Baoule of West Africa show this to the greatest degree, suggesting a possible correlation between size reduction and trypanotolerance (Spickett, 1994). Except for the humpless shorthorn Sheko breed of southwestern Ethiopia (Stein, 2011) and the Orma Boran cattle of Kenya's Tana Valley (Hanotte et al., 2003), East African cattle, on the other hand, show no more tolerance than those of European origin, implying a shorter history of exposure to trypanosomiasis, perhaps linked to greater admixture with/replacement by Asian/Middle Eastern-derived zebu cattle that lack resistance to the disease (Gifford-Gonzalez, 2000: 121–122). Collectively, sheep and goats display less pronounced trypanotolerance than cattle. In West and Central Africa the relevant trypanotolerant breeds are both dwarfed, with Djallonke sheep more resistant than West African Dwarf goats, but in East Africa neither Small East African goats nor Red Maasai sheep show reduced stature (Geerts et al., 2009). Experimental studies and observations

of imported European dogs suggest that some African dog breeds have also evolved resistance to *T. congolense* although how far this relates to size is uncertain (Mitchell, 2015).

### 2.2. African horse sickness

As its name implies, this is a major threat to horses. The eponymous virus finds its natural host in zebras, which are today endemic to sub-Saharan Africa, although the related taxa *Equus algericus* and *E. mauritanicus* are known from early Holocene contexts in the Maghreb (Faith, 2014). Midges of the genus *Culicoides* (especially *C. imicola*) are the principal vector. Mortality rates in horses are as high as 95% compared to 50% in mules (Coetzer and Guthrie, 2004). Donkeys, in contrast, mostly display subclinical signs, at least in sub-Saharan Africa, although mortality rates of up to 10% have been noted in the Middle East (Alexander, 1948). Since the African wild ass (*Equus africanus africanus*) populations from which donkeys derive (Mitchell, 2017b) show virtually no distributional overlap with extant zebras, might this hint that sub-Saharan donkeys too suffered from African horse sickness on first encounter before evolving the degree of immunity that they now possess?

Putting equids to one side, African horse sickness is also extremely dangerous to dogs, producing mortality rates of between 20% and 78% (Coetzer and Guthrie, 2004). Virtually all known outbreaks have been the consequence of ingesting horse meat, but van Sittert et al. (2013) document an instance where this can almost certainly be excluded, as well as providing references for *Culicoides* spp. possibly feeding on dogs, something that could provide a mechanism for direct infection via a non-oral route. The possibility that dogs can be infected with African horse sickness independently of consuming infected meat thus requires further investigation (see Fig. 2).

### 2.3. Wildebeest-derived malignant catarrhal fever (WD-MCF)

This condition is frequently fatal to cattle (Barnard, 1990), although instances of recovery and of infection without clinical signs developing are not uncommon. Hosted across eastern and southern Africa by blue (*Connochaetes taurinus*) and black (*C. gnou*) wildebeest, which are normally asymptomatic, it spreads from them via ocular and nasal secretions (including airborne transmission over short distances). Infected cattle cannot, however, then infect others (except transplacentally from mother to foetus). Although restricted in East Africa (where cattle pastoralism is common practice) to the open grasslands that wildebeest require, the considerable overlap between their dietary preferences and nutritional requirements and those of cattle mean that close interspecies interactions are all but unavoidable, especially during annual migration and synchronised calving events, though in the absence of wildebeest, sheep can act as the carrier for a related condition, sheep-associated malignant catarrhal fever. (Wambua et al., 2016) (see Fig. 3).

### 2.4. East Coast fever and Corridor disease

As with WD-MCF, the archaeological significance of these diseases was first highlighted by Gifford-Gonzalez (2000). Ticks (principally *Rhipicephalus appendiculatus*) spread the protozoa responsible for them, cattle-derived *Theileria parva* in the case of East Coast fever and buffalo-derived *T. parva* in that of Corridor disease. Like WD-MCF, horizontal transmission of Corridor disease between cattle does not normally take place, restricting the disease to places where cattle overlap with Cape buffalo (*Syncerus caffer*), which were ubiquitous historically in most savanna and many

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