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

Abstract

This paper summarises 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.

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 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, 2017).

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 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. 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.

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 the diversity of *Glossina* species that transmit them. In general terms, however, tsetse flies are found across some 10,000,000 km^2 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, but outside Africa have been reported to exhibit mortality rates of up to 10% (Alexander, 1948). Along with the lack of any significant distributional overlap between zebras and those African wild ass (*Equus africanus africanus*) populations from which donkeys derive (Mitchell, 2017), might this hint that they too suffered from African horse sickness on first encounter before evolving the degree of immunity that they now possess?

Finally, note that African horse sickness is also extremely dangerous to dogs, producing mortality rates of between 20% and 78% (Coetzer and Guthrie, 2004). Although virtually all such outbreaks have been the consequence of ingestion of horse meat, van Sittert et al. (2013) document an instance where this can almost certainly be excluded, as well as providing references for the possibility that *Culicoides* spp. may feed on dogs, which could provide a mechanism for direct infection via a non-oral route. Other potential vectors such as mosquitoes and ticks (including the brown dog tick, *Rhipicephalus sanguineus*) have also been suggested and in some cases have been shown to be capable of transmitting the disease, though their epidemiological importance remains unknown (Dardiri and Salama, 1988; Alexander et al., 1995; van Sittert et al., 2013). The possibility that dogs can be infected with African horse sickness independently of consuming infected meat thus requires further investigation.

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 inter-species 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 the related condition, sheep-associated malignant catarrhal fever. (Wambua et al., 2016).

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, Cape buffalo (*Syncerus caffer*) having been ubiquitous historically in most savanna and many rainforest environments south of the Sahara. Like WD-MCF, horizontal transmission of Corridor disease between cattle does not normally take place, restricting the disease to places where buffalo and cattle overlap. In those areas, however, fatality rates for cattle lacking resistance are in the order of 95–100%. East Coast fever is less virulent, but even with contemporary veterinary prophylactic care and tick control measures it still kills up to one-fifth of all East African calves (Ocaido et al., 2009), with mortality rates as high as 90% reported for cattle with no prior experience of exposure (Lawrence et al., 1994). Sheep and goats are susceptible, but less severely so. Indigenous African ‘Sanga’ cattle breeds of both humped (e.g. Afrikander) and humpless (e.g. Ankole) varieties have evolved higher levels of tick resistance than newly imported European breeds and also show greater tolerance of *T. parva* when infected (Spickett, 1994; De Castro et al., 1997).

2.5 Babesiosis (canine and equine)

Piroplasmid organisms of the genus *Babesia* parasitise many mammals. Two are particularly relevant. *B. rossi*, which is restricted to sub-Saharan Africa and spread by the southern African yellow dog tick (*Haemaphysalis elliptica*) and its more northerly cousin *H. leachi*, infects the red blood cells of dogs to produce a malaria-like condition that is frequently fatal, even with modern veterinary care (Defauw et al., 2012). Ubiquitous in tropical and southern Africa, the ticks infest not just dogs, but also all three sub-Saharan wild canids, the side-striped and black jackals (*Canis adustus*, *C. mesomelas*) and the African hunting dog (*Lycaon pictus*) (Penzhorn, 2011). Since these animals show no overt signs of infection the pathogen probably jumped from them to a new host when dogs first arrived south of the Sahara (Mitchell, 2015). Native dog breeds in at least two parts of Africa — South Africa (Maggs and Sealy, 2007) and Nigeria (Adamu et al., 2014) — have evolved a degree of resistance to *B. rossi*.

A related species of *Babesia*, *B. caballi*, is one of two piroplasmid agents (the other being *Theileria equi*; Wise et al., 2013) responsible for producing babesiosis (or piroplasmosis) in domestic equids, a condition that has been described as “the most serious infectious disease of horses in southern Africa” (Littlejohn and Walker, 1979: 309). A wide range of ticks act as vectors for these two parasites and *T. equi* at least seems to have first evolved as an infection of zebras, which now carry the disease (Bhoora et al., 2009; Hawkins et al., 2015). Accounts of equine babesiosis in donkeys are more limited than for horses and vary in the extent of pathogenicity noted: in contemporary Kenya the condition is, at worst, chronic, but may not produce any clinical signs, consistent with an evolution of immunity over time (Oduori et al., 2015). However, in Botswana and South Africa some reports suggest that donkeys may be just as susceptible as horses (Bowhill, 1905; Segwagwe et al., 2000).

2.6 Canine monocytic ehrlichiosis and heartwater

Both these diseases are caused by rickettsias of the genus *Ehrlichia*. *Ehrlichia canis*, the pathogen responsible for the first, is only effectively transmitted by the brown dog tick, *Rhipicephalus sanguineus*, which is found worldwide, but is particularly well adapted to Africa as it resists aridity and desiccation in temperatures of up to 35˚C and relative humidities of as little as 35%. Found in every African country, it has specialised to feed on dogs. Infected individuals normally show apparent recovery followed by further chronic symptoms after an initial acute phase, but effects are significantly worse if they are already infected with other pathogens. Dogs from breeds with no previous history of exposure can suffer mortality rates of 44–75% if left untreated. Conversely, Africa’s wild canids show few, if any symptoms when infected, and black-backed jackals also host *R. sanguineus* (Price and Karstad, 1980). Once again, this suggests a disease that has jumped species into domestic dogs.

In South Africa a second pathogen capable of producing canine ehrlichiosis-like symptoms is closely related to *E. ruminantium*, a clade of several organisms some of which cause heartwater (cowdriosis) in ruminants, although the symptoms of heartwater itself are quite different (Allsopp and Allsopp, 2001). Endemic to sub-Saharan Africa, this disease is hosted by wild antelope and is transmitted by ticks of the genus *Amblyomma*. Cattle, sheep, and goats all experience severe disease, with mortality rates of up to 90%, although indigenous African breeds (especially of caprines) are slightly less susceptible (Allsopp, 2010).

3. The constraining role of disease

African societies have not been passive in the face of these threats, using burning and browsing goats to help clear tsetse-infested bush and thus reduce the danger of trypanosomiasis infecting their animals or attempting to avoid contact between their cattle and wildebeest (Gifford-Gonzalez, 2000, 2016), although in at least one well-known historical instance forest clearance had the perverse consequence of introducing trypanosomiasis to an area (Freetown, Sierra Leone) from which it had previously been absent (Dorward and Payne, 1975). In this and other cases, however, there can be little doubt that infectious disease has helped shape the history of domestic mammals in sub-Saharan Africa. Its impact is perhaps most obvious with respect to the chronology of the spread of livestock in West Africa where, after a relatively rapid expansion across the modern Sahara during the mid-Holocene African Humid Period (di Lernia, 2013), the advance of cattle- and caprine-keeping pastoralists stalled between the sixth and mid-third millennia BC some 17˚N of the Equator. The oldest evidence of domestic cattle (*c*. 2600 cal. BC) further south comes from Karkarichinkat in Mali’s Tilemsi Valley (Manning, 2011), followed by a more broadly based expansion of cattle and caprines south of the River Niger and into northeastern Nigeria and Ghana from the first half of the second millennium BC (Linseele, 2013). Dogs show a similar pattern. Present in the central Sahara *c.* 4500 cal. BC (perhaps as part of a single, expanding pastoralist package; Gautier, 2002), they only seem to have reached beyond 22˚N after 2000 cal. BC, but even then are not documented south of the Niger or in the West African forest zone before the Christian era (Mitchell, 2015).

Contraction of rainfall belts toward the Equator between 4000 and 2500 cal. BC and the concomitant southward retreat of conditions suitable for the tsetse flies that are the primary vectors for trypanosomiasis almost certainly help explain this pattern. As Linseele (2013: 157) comments, however, caprines and cattle (Gautier and Van Neer, 2005) from early second-millennium cal. BC Kintampo Complex sites near the forest's northern margins in central Ghana imply that livestock spread rapidly once this contraction was underway. West African cattle do, indeed, show size reductions after 2000 BC that may be linked to trypanotolerance (MacDonald and MacDonald, 2000), but dwarf goats are not yet securely identified before 1000 cal. BC (Linseele, 2013: 159).

Domestic equids merit separate consideration. Donkeys are a puzzle as they were present in the central Sahara by the late second millennium BC (di Lernia et al., 2013), but are unknown in the trypanosomiasis-free grasslands of the Sahel before the early centuries AD (MacDonald and MacDonald, 2000). Horses, too, do not appear there before the mid-first millennium cal. AD. Once present, however, both species became important, one as a source of prestige and military power, the other as a beast of burden and key component of the commercial networks linking the Sahel with the Sahara to its north and the rainforests to its south (Mitchell, 2005). Trypanosomiasis did, however, severely constrain their southward expansion: neither donkeys nor horses could survive for long in West Africa's forest zone, leaving states like Oyo in central Nigeria and Gonja in northern Ghana to rely almost entirely on horses imported from the north for their cavalry (Law, 1976).

On the opposite side of Africa the initial spread of livestock into northern Kenya *c.* 3000-2500 cal. BC shows a striking degree of contemporaneity with events in West Africa. Sheep and goats were kept first, with cattle only appearing *c.* 1700 cal. BC. Though the immediate source areas (South Sudan and southern Ethiopia) remain archaeologically almost unknown, it is again likely that contraction of rainfall belts, and thus of the trypanosomiasis zone, facilitated movement south, perhaps via a temporarily tsetse-free corridor along the Bahr el-Ghazal drainage (Gifford-Gonzalez 2000: 121). The caprines-before-cattle pattern itself may also reflect the added dangers posed to cattle by the widespread presence of wildebeest-derived malignant catarrhal fever, East Coast fever, and Corridor disease (Gifford-Gonzalez 2000, 2016). Donkeys, the fourth domestic mammal associated with early pastoralists in East Africa are currently unknown before *c.* 1000 cal. BC, implying a later entry; trypanosomiasis (which historically effectively confined them to arid and semi-arid areas of Kenya, northern Uganda, and northern Tanzania, preventing them from spreading further south or toward the Great Lakes; Wilson 2013) and — until a degree of immunity had evolved — perhaps also African horse sickness and equine piroplasmosis may be implicated here.

Dogs, though kept as far south as 15˚N as early as 4000 cal. BC, arrived in East Africa much later than livestock: they are archaeologically unknown before the second half of the first millennium cal. AD, when they appear in contexts associated not with pastoralists, but with Iron Age communities who practised mixed farming. This could reflect a different set of trypanosomal threats (*T. b. brucei* and *T. congolense* rather than *T. congolense* and *T. vivax*), but we should also ask whether dogs experienced greater difficulty than ruminants in evolving trypanotolerance as a whole.

Across Central Africa cattle — which principally eat grass, but would also have been exposed there to trypanosomiasis *and* East Coast fever — were not kept in the equatorial rainforests, although goats were, with sheep present in some areas on the forest margins (Vansina, 1990). In both cases trypanotolerant breeds were kept, but as in comparable rainforest environments in West Africa the growth rate of dwarfed sheep is slower and the mortality of their offspring higher compared with dwarfed goats, suggesting greater vulnerability to trypanosomiasis (Connor, 1994). Linguistic reconstructions imply that goats (and dogs) arrived in Central Africa during the first millennium BC as part of the expansion of Bantu-speaking horticulturists who grew yams, oil palm, and (a little later) plantain (Vansina, 1990: 92). Details remain vague, but the available data support movement south through the Atlantic forest prior to colonisation of the Congo River and its tributaries (de Maret, 2013).

To the east of the rainforest, the expansion of livestock stalled again for the best part of a millennium just south of Tanzania’s Lake Eyasi around 3000 BP. No sites attributable to East Africa’s Pastoral Neolithic cultures have been confirmed beyond 5˚S and the oldest (caprine) livestock from southern Africa do not predate the third/fourth centuries cal. BC (Pleurdeau et al., 2010). The antiquity of cattle in northern Botswana (2070±40 BP, 162 cal. BC – cal. AD 75, Beta-1904888; Robbins et al., 2008) may, however, mean that what seems on the surface like a recurrence of the East African caprines-before-cattle pattern (Gifford-Gonzalez, 2016) is no more than an artefact of sampling. Donkeys, on the other hand, which were kept by some Pastoral Neolithic groups, did not make it south (Mitchell, 2017), not even when Khoekhoe pastoralists of ultimately East African origin were joined in southern Africa by agropastoralist Iron Age groups with both East and Central African roots (Huffman, 2007).

Disease may have influenced this situation in several ways. First, the geographical overlap and combined effects of East Coast fever, Corridor disease, wildebeest-derived malignant catarrhal fever, and trypanosomiasis provide a plausible explanation of the delayed expansion of livestock beyond the open grasslands of northern Tanzania into the denser savannas of south-central Africa (Gifford-Gonzalez, 2000). But second, on entering the more arid regions south of the Caprivi Strip and Okavango Delta early herders and their animals will have found themselves in areas where those diseases (and many of their hosts) were less prevalent: combined with a milder and (near the Atlantic coast) wetter Neoglacial climate, this may have facilitated a rapid expansion into western South Africa (Orton et al., 2013). Third, donkeys could have been excluded from the southward spread of livestock if people keeping domestic mammals chose to move through and settle (however temporarily) in areas with a reduced threat from *T. brucei* (which is frequently fatal to donkeys) rather than *T. congolense* and *T. vivax*, which are less serious for donkeys but pose significantly greater dangers to cattle and caprines (Namangala and Odongo, 2014: 244). Fourth, the broad contemporaneity of the first evidence for dogs in southern Africa with their earliest appearance in East Africa could reflect a delayed evolution of tolerance for trypanosomiasis as proposed above, followed by a rapid release from this constraint once this had been gained. That dogs (which postdate livestock in southern Africa by 700 years or more) — like donkeys (which never reached the region) — are most at threat from *T. brucei*, rather than other tsetse-spread trypanosomes, adds an intriguing twist to this suggestion, but sits uncomfortably with their apparent presence among Bantu-speaking societies in the Congo Basin and the forests to its north and west (Vansina, 1990: 83). The discrepancy underlines the need for both a larger archaeological dataset and better knowledge of canine genetics.

4. Discussion

4.1 Taking the argument further

The proposition that infectious diseases endemic to sub-Saharan Africa influenced and constrained the spread of domestic mammals originating outside the region depends upon several assumptions (Gifford-Gonzalez, 2000; Mitchell, 2015). These include:

1. The diseases discussed have the requisite degree of antiquity;

2. The relevant hosts and vectors were present in the appropriate places and at the relevant times for the pathogens they support to infect domestic mammals;

3. Where domestic mammals are susceptible to pathogens that also infect wild animals, but at much lower levels of pathogenicity, this is because the former have a more recent history of exposure;

4. Where some breeds show tolerance to particular pathogens but others do not, this must have taken time to evolve and the disease in question was therefore once a greater threat than it is today.

The first of these assumptions is essentially a matter of pathogen evolution, while the second requires us to reconstruct the ecological conditions relevant to pathogen presence or absence, as well as to be confident that we have a robust understanding of the past distributions of domestic mammals. The others flow from general understandings of disease-host relations. Direct evidence for any of them in the archaeological record is challenging, but not impossible. In the most favourable conditions pathogen vectors can be detected, as exemplified by the presence of brown dog ticks and other parasites in a mummified dog from Roman Egypt (Huchet et al., 2013). Notwithstanding current debate over the accuracy of recent faunal identifications from late Holocene contexts in southern Africa (Horsburgh et al., 2016 cf. Bousman et al., 2016; Scott and Plug, 2016), continuing advances in the recovery and analysis of ancient DNA (cf. Bodiba, 2015 and Gallego Llorente et al., 2015 for human remains) also hold out the promise that some pathogens may prove to be directly identifiable, something already accomplished elsewhere with respect to people (e.g. Aufderheide et al., 2004; Lima et al., 2008; and see Harkins and Stone 2014 for a more general review).

Analysis of the genomes of African breeds of domestic mammals and of individual pathogens should also prove revealing. Initially, for example, Gifford-Gonzalez (2000) suggested that Rift Valley Fever (a mostly mosquito-borne viral infection) also constrained the spread of domestic livestock south of the Sahara. However, the genetic diversity of the virus responsible coalesces no earlier than the late nineteenth century (Bird et al., 2007), removing it from consideration as a limiting factor on the expansion of cattle and caprines in prehistory (Wright, 2011). Future work may also establish the precise genetic basis for trypanotolerance and other forms of pathogen resistance (Yaro et al., 2016) and help ascertain if African breeds have passed through genetic bottlenecks that might reflect exposure to pathogens at earlier stages in their evolutionary history (cf. Mbole-Kariuki, 2014 with respect to the impact of the late nineteenth-century rinderpest pandemic on East African cattle).

Until such data are obtained studies of the impact of infectious disease on the expansion of domestic mammals in sub-Saharan Africa will continue to rely upon demonstrating that the relevant hosts were present in a particular time and place and/or that the key vector species did so. Previously, this has depended upon extrapolating from current/historic distributions of host species such as wildebeest and Cape buffalo (Gifford-Gonzalez, 2000) or of the tick and fly vectors responsible for diseases like trypanosomiasis and canine babesiosis (Smith, 1992, 72–73; Mitchell, 2015). Principally perhaps because of the limited resolution of the available palaeoenvironmental evidence, archaeologists' modelling of such distributions and of thus of their influence on when and where particular domestic taxa could have been kept or moved has often been broad-brush. This is, however, now starting to change. Recently, for example, Chritz et al. (2015) used several environmental proxies, particularly stable isotope analysis of wild and domestic fauna dated to 1900–1600 BP at the site of Gogo Falls, to argue for a tsetse-free area extending from western Kenya toward northern Tanzania. However, their conclusion that this "provide[s] empirical evidence for the existence of a grassy corridor through which small groups of herders could have passed to reach southern Africa" is belied by the fact that their data are ≥300 years *younger* than the first arrival of livestock south of the Zambezi. Recently published isotopic evidence from Makwe Rockshelter in southeastern Zambia, located almost midway between northern Tanzania and Toteng 1, the earliest site to have produced both cattle and sheep in southern Africa (Robbins et al., 2008), is likewise handicapped. As its authors admit, the relevant (1600–800 BP) sediments "postdate the initial movements of herders across the region" and arguments that "our data are within hundreds of years of this event (*sic*) and it is possible, if not likely, that similar environments persisted at that earlier time" (Robinson and Rowan, 2017) fail to reassure.

But if neither the Gogo Falls nor Makwe studies are directly relevant to understanding how domestic mammals expanded through sub-Saharan Africa at a regional scale, their focus on individual sites and relatively short spans of time in what may have been key zones for the movement of livestock and people, and their deployment of techniques hitherto rarely used to address these questions, do point the way forward. For some diseases a focus on documenting the past presence of key reservoir species will also be useful, particularly for plains zebra (*Equus quagga*; African horse sickness; horses), blue and black wildebeest (wildebeest-derived malignant catarrhal fever; cattle), and Cape buffalo (Corridor disease; cattle). With due regard to close dating and potential sampling and identification biases, datasets of past mammal distributions (e.g. Plug and Badenhorst, 2001) could help identify where and when such reservoir taxa appear in the archaeological record and thus when and where opportunities existed for domesticates to expand in their absence.

4.2 The consequences of disease

The diseases discussed above had manifold impacts on when and where people could keep domestic mammals south of the Sahara. Some of the most direct involved the subsistence strategies they practised and, perhaps, the resilience of those strategies to drought or other risks, for where diseases such as trypanosomiasis or East Coast fever limited, or precluded, the keeping of cattle, for example, people had little choice but to go without the meat and dairy resources that they might otherwise have provided. At a sub-continental level this meant that rainforest-dwelling populations in Central Africa, as well as many of those living in similar environments in West Africa or the woodland savannas of Zambia, Katanga, Malawi, and Tanzania, secured much of their protein not from livestock, but from hunting and trapping bushmeat (including animals attracted to garden plots) or fishing (Vansina, 1990: 89–92; Gautier and Van Neer, 2005; Linseele, 2013: 160; Connah, 2016: 188). At the local scale, this is evident archaeologically at sites like Kadzi on the Zambezi where hunting buffalo and impala (*Aepyceros melampus*) was particularly important in the first millennium AD but livestock keeping restricted in scope, probably because of trypanosomiasis and other diseases (Plug, 1997). For similar reasons, some, but not all, Early Iron Age sites in Kruger Park, South Africa, document a similar pattern (extended here to include blue wildebeest and plains zebra), though the range and intensity of tsetse-infestation has undoubtedly varied over the past 2000 years (Plug, 1989; and see Badenhorst, 2008 for a critical re-evaluation of the impact of disease).

Keeping animals is never, however, just a matter of procuring meat, but encompasses their place in human social relations, as well as the secondary products (dairy foods, traction, transport etc.) that they offer. For Eastern Bantu speakers in eastern and southern Africa, for example, marriage typically required the exchange of bridewealth in the form of cattle (Huffman, 1998). Lacking cattle, most Western Bantu speakers therefore arranged marriages not via payments in livestock but by the groom working for the bride’s family (Colson and Gluckman, 1951). Importantly, cattle were also a self-perpetuating, increasable resource that allowed wealth to be accumulated, stored, and converted (into women as wives, but also, for example, into political loyalty through systems like the *mafisa* of southern Africa’s Sotho-Tswana speakers; Delius, 1983; Kazankov, 2003). Their manipulation in sustaining acts of conspicuous consumption is also well documented (Barker, 1988).

In similar vein, the use of horses as cavalry in the Sahel has been thought of as pivotal in the formation of territorially extensive states and empires (Goody, 1971) and, even if their military advantages and associations with centralised polities are questionable, their value in differentiating elites and acquiring slaves is not in doubt (Haour, 2007). Significantly enough, polities of a scale comparable to medieval Mali or Songhay did not form in either eastern or southern Africa, areas where horses were absent. Indeed, even when introduced to South Africa by Europeans after 1652, African horse sickness and (in wetter areas) trypanosomiasis constrained military operations and precluded the development of equine-based transport systems, leaving oxen, for example, to pull Boer wagons into the interior (Brown, 2008). Disease challenges likewise made it impossible for Europeans to deploy cavalry against the polities they encountered on the coasts of West and Central Africa, one of several constraints on their colonisation of these regions until well into the nineteenth century (Thornton, 2012: 182). African horse sickness, in particular, also helps explain the very limited (and geographically circumscribed) extent to which — unlike the Americas — Indigenous equestrian hunting and raiding societies developed in southern Africa (Mitchell, 2016). Finally, it is worth noting how for lack of donkeys Khoekhoe pastoralists had to use slower, energetically less efficient, nutritionally more demanding oxen to move their homes and goods, while elsewhere in southern and south-central Africa — just as in the rainforests — the same lack meant that trade items and agricultural produce could only be carried overland (and then in significantly smaller quantities) on people's heads (Mitchell, 2017).

4.3 African diseases beyond Africa

Like trade goods, diseases have been important components of the connections linking Africa to other parts of the world (Mitchell, 2005). I single out two examples, one specific to equids and of some considerable antiquity, the other a broader set of infections spread to the Americas after Columbus.

As well as *T. b. brucei*, donkeys and horses are susceptible to two other trypanosomal diseases, one of which — surra — is also a serious disease of dogs and camels, though the other — dourine — is restricted to equids. The pathogens concerned (*T. b. evansi* and *T. b. equiperdum* respectively) cannot be spread by, or survive in, *Glossina* spp. (Birhanu et al., 2016). Instead, blood-eating flies (*Stomoxys* spp., *Tabanus* spp.) transmit the first, while the second is almost exclusively passed on during mating as it lives in the animals' genitalia. Both conditions produce high mortality rates: for surra up to 100% in dogs and over 50% in naïve horse populations, for dourine up to 50–70% (Desquesnes et al., 2013). Within Africa surra is nevertheless today principally an infection of camels, which presents a problem as they are not attested there before the first millennium BC and did not reach the southern margins of the Sahara until the third century cal. AD (MacDonald and MacDonald, 2000). The difficulty is twofold: first, surra is apparently recorded in India in the mid-first millennium BC (Hoare, 1972) and second, *T. b. brucei*, from which *T. b. evansi* and *T. b. equiperdum* evolved on multiple occasions (Carnes et al., 2015), is a purely sub-Saharan pathogen, just like its tsetse fly vectors, meaning that both surra and dourine must have developed *within* Africa.

Although phylogenetic analyses have not yet proposed a chronology for these evolutionary events except to suggest that they were "recent" (Wen et al., 2016: 58–59), I propose four grounds for thinking that donkeys may provide an appropriate vehicle for the initial development and out-of-Africa expansion of both surra and dourine. First, donkeys, which are native to Northeast Africa, had certainly penetrated parts of sub-Saharan Africa where trypanosomiasis is likely to have been present before 1000 cal. BC (Kimura et al., 2013). Second, unlike most other domestic animals they are primarily kept as beasts of burden and for riding, making them ideally suited for use in long-distance transport networks and thus able to transmit *T. b. equiperdum* and *T. b. evansi* within Africa and beyond (Marshall, 2007). Third, they experience milder symptoms than horses (or camels) when infected by surra or dourine, implying a longer history of exposure to the responsible pathogens (Desquesnes et al., 2013). And finally, dourine is more readily transmitted from stallions to mares, rather than the reverse, consistent with *T. equiperdum* infecting horses as a result of crossbreeding male donkeys (which can be asymptomatic carriers) with mares to produce mules (Center for Food Security & Public Health 2015).

Surra also features in my second example, the transmission of African diseases to the New World. Today, it occurs widely across Central and South America, infecting mammals as diverse as guanacos (*Lama guanicoe*), jaguars (*Panthera onca*), and coatis (*Nasua nasua*) and finding local hosts in vampire bats (*Desmodus rotundus*) and possibly capybaras (*Hydrochaeris hydrochaeris*) (Desquesnes et al., 2013). Introduction by the horses of Spanish or Portuguese *conquistadores* is likely (Hoare, 1965) and horses — along with dogs — are its principal victims. Surra is not, however, Africa's only animal pathogen gift to the Americas. Canine monocytic ehrlichiosis, for example, is now among the most important canine diseases in Brazil (Labruna et al., 2007), with both its pathogen (*Ehrlichia canis*) and vector, the brown dog tick (*Rhipicephalus sanguineus*) post-Columbian introductions (Szabó et al., 2005). Canine babesiosis and visceral leishmaniasis caused by infection with *Leishmania infantum* (*chagasi*) (not discussed here, but a disease of both dogs and people; Mitchell, 2015) can be readily added to this list, with genetic evidence confirming their exotic — ultimately sub-Saharan — origin (Eiras et al. 2008; Leblois et al. 2012). So too can *Trypanosoma vivax*, which in the absence of *Glossina* spp. is transmitted by biting flies. Now a major disease of ruminant livestock in much of South America, it was probably brought to the Americas by cattle from Senegal and the Gulf of Guinea in the early 1700s (Gonzatti et al., 2014). No full consideration of the economic, ecological, and human impacts of Crosby's (1986) Columbian Exchange can exclude it or the other diseases I have mentioned.

5. Conclusion

A multiplicity of diseases endemic to sub-Saharan Africa and, in several cases, hosted by close relatives of the domestic mammals introduced there from outside, have constrained the expansion and keeping of ruminant livestock, dogs, horses, and donkeys south of the Sahara. These constraints have, in turn, shaped the cultural and political life of African populations, as well as influencing the subsistence strategies they have practised. Additionally, both before and after Europe's voyages of discovery they have formed part of the connections linking Africa with other parts of the world. Importantly, however, the diseases reviewed here do not exhaust those that exist. I have not, for example, discussed pigs, although the devastating impact of African swine fever, a tick-borne disease hosted by warthogs (*Phacochoerus* spp.), bushpigs (*Potamochoerus* spp.), and giant forest hogs (*Hylochoerus meinertzhageni*) that produces mortalities of up to 100% in domestic pigs (Penrith, 2009), provides a ready suid parallel for African horse sickness and canine babesiosis. Additionally, pigs also suffer from their own (very acute and generally fatal) form of trypanosomiasis; as with African swine fever, the pathogen, *T. simiae*, has bushpigs and warthogs as its principal hosts (Isoun, 1968; Pollock, 1982: 69). Although further research is warranted (including direct dating and, if possible, aDNA analysis of possible remains), archaeological, historical, and genetic evidence do not currently offer a strong basis for thinking that pigs were present in sub-Saharan Africa before

European contact (Blench, 2000; Gifford-Gonzalez and Hanotte, 2011). Given that its natural hosts are endemic to and widely distributed across Africa south of the Sahara, could African swine fever help explain this and why pigs struggled to establish themselves thereafter? Both with respect to this example and the other species I have discussed, there is clearly much still to learn about how infectious disease influenced the spread of domestic mammals through sub-Saharan Africa, the co-evolutionary history between them, and the strategies African societies employed to mitigate their effects.

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