

REVIEW

Carnivory in the common hippopotamus *Hippopotamus amphibius*: implications for the ecology and epidemiology of anthrax in African landscapes

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Keywords

anthrax, carnivory, hippopotamus, predation, scavenging

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Submitted: 21 May 2015

Returned for revision: 9 July 2015

Revision accepted: 20 October 2015

Editor: KH

doi:10.1111/mam.12056

ABSTRACT

1. The common hippopotamus *Hippopotamus amphibius* ('hippo') is a keystone species whose foraging activities and behaviour have profound effects on the structure and dynamics of terrestrial and aquatic ecosystems within its habitat.
2. Although hippos are typically regarded as obligate herbivores and short-grass grazing specialists, field studies have demonstrated that hippos are facultative carnivores that consume flesh and intestinal tissues from the carcasses of other animals. Carnivory by hippos is not an aberrant behaviour restricted to particular individuals in certain localities, but a behaviour pattern that occurs within populations distributed in most of the hippo's current range in eastern and southern Africa. Carnivory is frequently associated with communal feeding involving multiple individuals or entire social groups of hippos.
3. The observed tendency of hippos to feed on carcasses, including those of other hippos, has important implications for the ecology and epidemiology of anthrax and other ungulate-associated zoonotic diseases in African landscapes. Scavenging and carnivory by hippos may explain why the spatiotemporal patterns and dynamics of anthrax mortality among hippos often differ markedly from those of other anthrax-susceptible herbivores within the same habitats, and why levels of hippo mortality from anthrax may be orders of magnitude higher than those of other anthrax-susceptible ungulate populations within the same localities.
4. Recognition of the role of carnivory as a key factor in modulating the dynamics of mass anthrax outbreaks in hippos can provide a basis for improved understanding and management of the effects of anthrax outbreaks in hippo and human populations.

INTRODUCTION

The common hippopotamus *Hippopotamus amphibius* ('hippo') is an ecological keystone species whose activities have significant impacts on landscape structure and dynamics within its habitats. Hippos affect the hydrology and geomorphology of aquatic and wetland ecosystems, the physical structure and species composition of plant communities in terrestrial ecosystems, and nutrient exchange between terrestrial and aquatic ecosystems (Field 1970, Olivier & Laurie 1974, Ellery et al. 2003, Subalusky et al. 2015). The hippo is typically characterised as an obligate herbivore and short-grass grazing specialist, whose diet may include limited amounts of aquatic macrophytes, dicotyledonous herbaceous plants, and woody plant browse (Owen-Smith 1988, Eltringham 1999).

The behavioural ecology of hippos is complex: individuals are typically solitary when foraging but highly gregarious and territorial in their diurnal aquatic habitats. Hippos forage primarily at night, during excursions from, or between, bodies of open surface water (lakes, rivers, and pans) in which most of the daylight hours are spent (Laws 1968). During dry seasons and drought periods when the availability of palatable vegetation near aquatic daytime schooling or resting areas is limited, hippos may range 4 km or more from water during nocturnal foraging excursions (Lock 1972, Kanga et al. 2013).

Hippo social groups are unstable aggregations comprised of individuals of mixed ages and sexes; depending on location and season, the size of hippo aggregations may number from a few individuals to as many as 100–150 individuals (Owen-Smith 1988, Eltringham 1999). Male and female hippos are often highly aggressive and have a documented ability and propensity for attacking and killing conspecifics, humans, and other large vertebrates on land and in water. Male hippos are aggressively territorial and fight for dominance, and may also attack subadults and juveniles (Kingdon 1982). Infantidal behaviour by adult male hippos has been documented (Lewison 1998), and aggression resulting in injuries and death can also occur between males and females, females and females, or adults and subadults or juveniles (Karstad & Hudson 1986). Aggression between hippos in savanna landscapes of eastern and southern Africa is often more frequent and intense during dry season periods, when hippos become concentrated within areas where water is still present (Olivier & Laurie 1974, Karstad & Hudson 1986). Although many instances of attacks by hippos on conspecifics or other species may be attributable to territorial behaviour, there are documented instances of hippos feeding communally on the carcasses of animals killed by members of their herds. They also feed on the carcasses of animals that may have been killed by crocodiles or mammalian predators, died of injuries sustained in

attacks by other animals, or died of disease or of other natural causes (Dudley 1996, 1998, Eltringham 1999, Steyn 1999, Dutton & Subalusky 2011, Dorward 2015; Fig. 1, Table 1).

Hippos are susceptible to a wide variety of bacterial and viral diseases and parasites, including anthrax, brucellosis, Rift Valley Fever, tetanus, trypanosomiasis, shistosomiasis, salmonellosis, trichinosis, roundworms, blood and liver flukes, and ticks (Heckel 1879, Garnham 1960, Cowan et al. 1967, de Vos & de Klerk 1980, Despres et al. 1995, Eltringham 1999, Bengis et al. 2002, Bekker et al. 2012). Mass outbreaks of anthrax occur periodically within hippo populations in Zambia and Uganda (Fig. 2). Hippos are immune to foot-and-mouth disease, a highly contagious viral disease of major economic importance that infects most species of artiodactyls, especially wild and domestic species of cattle and swine (Bengis & Erasmus 1988, Thomson et al. 2001). Hippos are resistant to rinderpest, a highly contagious and lethal viral disease of ruminants and suids (Plowright et al. 1964).



Fig. 1. Photographs of hippos feeding on carcasses from documented observations of carnivory reported in this study. (a) Hippo manipulating a wildebeest *Connochaetes taurinus* carcass at the Mara River during the wildebeest crossing in 2011. Note more wildebeest carcasses in the background. (photo courtesy of Christopher Dutton). (b) Hippos feeding communally on an impala *Aepyceros melampus* carcass at Masuma Dam in Hwange National Park in October 2014. Note the feeding postures of the hippos in the left foreground, and the mouth of the juvenile in the background on the left. The carcass has been separated into several different pieces. (photo courtesy of Julio de Castro).

Table 1. Ecological and ethological data for scientific records of carnivory by *Hippopotamus amphibius*

Location	Prey species	Date	Season	Communal feeding (n animals)	Anthrax outbreak	Reference
Masuma Dam, Hwange National Park, Zimbabwe	Impala (adult)	Jul 1995	Cold dry season drought	Yes (n > 6)	No	Dudley (1996, 1998)
Nyamandlovu Pan, Hwange National Park, Zimbabwe	Impala (adult)	Aug 1995	Cold dry season drought	Yes (n = 2)	No	Dudley (1996, 1998)
Chobe River, Chobe National Park, Botswana	Elephant (juvenile)	Nov 1995	Hot dry season drought	Yes (n = 5)	No	Steyn (1999)
Shire River, Liwonde National Park, Malawi	Hippo (adult)	Dec 1996	Early rainy season	No	No	Eltringham (1999)
Grumeti River, Serengeti National Park, Tanzania	Hippo (juvenile)	Dec 2001	Dry season drought	No	No	Woodford (2004)
Kazungu Channel, Queen Elizabeth National Park, Uganda	Hippo (adult)	Dec 2004	Rainy season	No	Yes	Leendertz, this study
Mara River, Kenya	Wildebeest (adult)	Sept 2009	Dry season drought	Yes (n = 2)	No	Dutton and Subalusky (2011)
Mara River, Kenya	Wildebeest (adult)	Jul 2011	Dry season drought	Yes (n = 2)	No	Subalusky, this study
Luangwa River, South Luangwa National Park, Zambia	Hippo (adult)	Jul 2011	Hot dry season	Yes (n = 2)	Yes	Hang'ombe, this study
Luangwa River, South Luangwa National Park, Zambia	Hippo (adult)	Aug 2011	Hot dry season	Yes (n = 3)	Yes	Hang'ombe, this study
Luangwa River, South Luangwa National Park, Zambia	Hippo (adult)	Sept 2011	Hot dry season	No	Yes	Hang'ombe, this study
Luangwa River, South Luangwa National Park, Zambia	Hippo (adult)	Oct 2011	Hot early rainy season	No	Yes	Hang'ombe, this study
Zambezi River, Lower Zambezi National Park, Zambia	Hippo (adult)	Oct 2011	Early rainy season	Yes (n = 5)	Yes	Hang'ombe, this study
Luangwa River, South Luangwa National Park, Zambia	Hippo (adult)	Oct 2012	Hot early rainy season	Yes (n = 3)	No	Hang'ombe, this study
Luangwa River, South Luangwa National Park, Zambia	Hippo (adult)	Oct 2013	Hot early rainy season	Yes (n = 5)	No	Hang'ombe, this study
Sabie River, Kruger National Park, South Africa	Hippo (adult)	Apr 2014	Late rainy season	No	No	Dorward (2015)
Masuma Dam, Hwange National Park, Zimbabwe	Impala (adult)	Oct 2014	Hot dry season drought	Yes (n > 10)	No	de Castro, this study

The role of hippos as potential sources for human infections with zoonotic diseases, and as keystone hosts for microbial pathogens, is an aspect of hippo ecology that merits closer investigation. In this study, we review and discuss the potential importance of the phenomenon of carnivory by hippos for the ecology and epidemiology of the anthrax bacterium *Bacillus anthracis* in sub-Saharan Africa.

FORAGING ECOLOGY

The hippo has been almost universally characterised in the scientific literature as a herbivore and grazing specialist whose diet consists mainly of grasses supplemented by limited amounts of aquatic macrophytes and non-graminoid herbaceous plants (Field 1970, Owen-Smith

1988, Dunham 1990, Mugangu & Hunter 1992, Eltringham 1999, Boissarie et al. 2005, Cerling et al. 2008, de Longh et al. 2011, Michez et al. 2013). Although grasses may be their preferred forage, isotope analysis of hair samples from wild hippos has documented dietary shifts between 100% C4 grasses and 100% C3 plants on a seasonal basis in some habitats (Cerling et al. 2008). Analyses indicate that much higher amounts of C3 biomass from dicotyledonous plant materials (sedges, forbs, aquatic macrophytes) are found in the hippo's diet than would be expected based on the literature (Grey & Harper 2002, Boissarie et al. 2005). This finding is supported by field studies that have shown that hippos may feed on dicotyledonous herbaceous plants and utilise lower nutrient aquatic plants during seasons when palatable higher quality terrestrial grasses are not available (Mugangu & Hunter 1992, Michez et al. 2013).



Fig. 2. Aerial view of hippo mortality in the Luangwa River, Zambia, during the 1987 anthrax outbreak. At least 50 carcasses of dead hippos (whitish/grey) and approximately 100 live hippos (brown/black) are visible in this photo. The many large birds visible roosting in trees and feeding on hippo carcasses are marabou storks *Leptoptilos crumenifer* (photo courtesy of Richard Bell).

The apparent avoidance of aquatic plants as food by the hippo is significant in light of the fact that hippos spend much of their lives in water, and may travel long distances away from water in nocturnal foraging excursions in search of palatable forage (Eltringham 1999). Comparative studies of sympatric ungulates with different foraging habits have shown that the dietary carbon $\delta^{13}\text{C}$ isotope ratio of the hippo is intermediate between those of true obligate grazing species (hartbeest *Alcelaphus buselaphus*, wildebeest *Connochaetes taurinus*, African buffalo *Synacerus caffer*, zebra *Equus quagga*, waterbuck *Kobus ellipsiprymnus*, and warthog *Phacochoerus africanus*) and those of obligate browsers (giraffe *Giraffa camelopardalis*, dik-dik *Madoqua* spp.); the degree of overlap between the isotope ratio of hippos with the obligate grazers indicates the importance and seasonal dominance of grasses in the hippo's diet (Cerling et al. 2008).

There are a growing number of documented instances of wild hippos feeding on the carcasses of animals killed by other hippos, crocodiles, or other predators, and of animals that may have died of natural causes (Dudley 1996, 1998). Documentation includes online photographs and videos (e.g. <http://www.dailymail.co.uk/news/article-2687478>, <http://www.youtube.com/watch?v=fGYVZdASgUw>, <http://www.serengeti-wildlife.com/2015/10/15/never-seen-before-rare-image-series-about-a-hunting-hippopotamus/>) as well as published reports of hippos consuming the flesh or internal organ tissues or both of a broad suite of large mammal taxa, including, but not limited to hippos, impalas *Aepyceros melampus*, elands *Taurotragus oryx*, elephants *Loxodonta africana*, kudus *Tragelaphus strepsiceros*, wildebeest, African buffalo, and zebras (Crowther & Whyte 1989, Dudley 1998, Eltringham 1999, Steyn 1999, Dutton & Subalusky 2011, Dorward 2015). There are also reports of captive hippos in

zoos killing and eating a wide variety of vertebrate taxa, including a pygmy hippo *Chorelopsis liberiensis*, a Malaysian tapir *Tapirus indicus*, a wallaby *Macropus rufogriseus*, as well as flamingos *Phoenicopterus* spp. and several other species of birds (Frost 1996, M. Clauss unpubl. obs.). During the past two decades, we have documented observations of hippos feeding on a wide array of ungulate taxa, including hippos (Table 1), at locations that encompass much of the species' current geographic range (Fig. 3). While the actual ingestion of animal tissues by hippos feeding in water is often difficult to observe or photograph (see Fig. 1), we have documented unequivocal instances of this behaviour at many sites in southern and eastern Africa (Table 1). Our scientific records, coupled with those of other investigators and observers, demonstrate that the phenomenon of carnivory by hippos is not restricted to particular individuals or local populations but is an inherent characteristic of the behavioural ecology of hippos.

DIGESTIVE ANATOMY AND PHYSIOLOGY

The hippo is one of the world's largest living terrestrial mammals, with an adult body mass of up to 2500 kg (Owen-Smith 1988). The hippo's robust mandible, hypertrophied canine teeth, and wide mouth gape have evolved under strong selection for use as display organs and weapons for intraspecific dominance fighting (Kingdon 1982), and have no primary functions in feeding on plant materials (Laws 1968). The interlocking canines of hippos constrain lateral grinding chewing motion, which is probably why hippos have relatively poor mastication efficiency compared with most other ungulates (Fritz et al. 2009). The extremely wide mouth gape of hippos (nearly 180°) is an

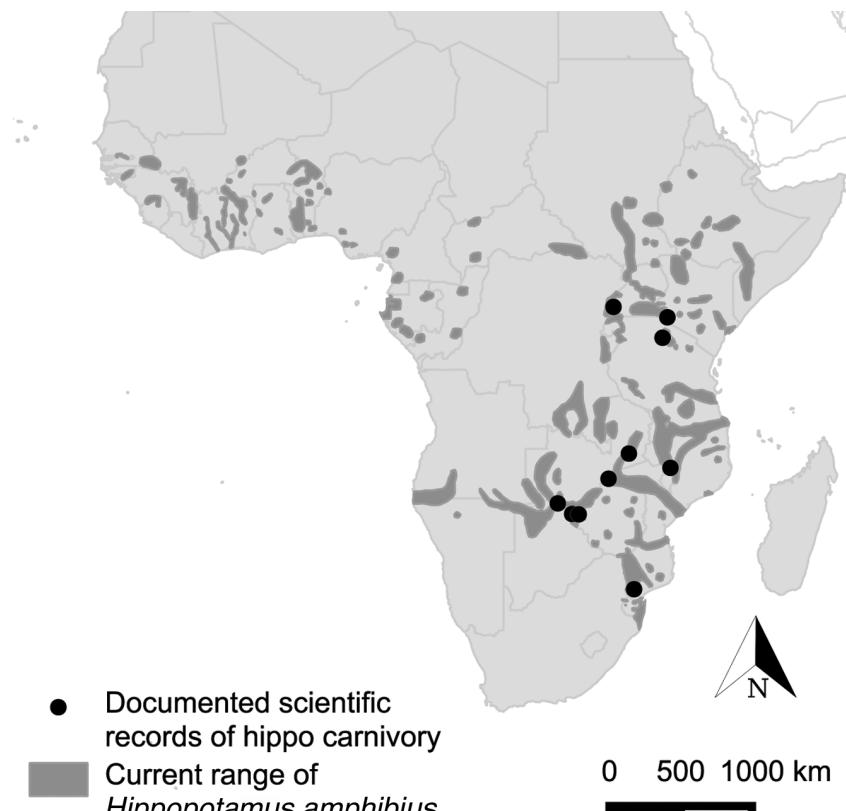


Fig. 3. Map of the current range of the hippo *Hippopotamus amphibius* in sub-Saharan Africa, showing locations where instances of carnivory by hippos have been documented in Table 1. (Range Map data courtesy of IUCN Red List, accessed 5 May 2015).

anomaly among grazing ungulates and is more characteristic of that associated with mammalian carnivores (Herring & Herring 1974). Hippos are believed to have an unusually low metabolic rate for a terrestrial mammal of their size, coupled with a relatively low food intake rate for a herbivorous ungulate species. The average dry matter intake of forage by wild hippos has been estimated to be 0.5–1.5% of their body mass per day (Field 1970, Arman & Field 1973) or approximately 37 g kg^{-1} body mass $^{0.75}$ (Clauss et al. 2004, 2007, Schwarm et al. 2006), which can translate to 6 g dry matter/kg body mass/day for an average hippo (Subalusky et al. 2015). In hippos, increased levels of forage intake are correlated with an accelerated rate of gut-content passage through the digestive tract, which limits the amount of additional nutrients or energy that can be obtained by increasing forage intake; these factors could help explain the comparatively low food intake and short feeding times exhibited by hippos (Clauss et al. 2007).

The hippo is the largest extant terrestrial mammal that possesses a foregut fermentation digestive system. All other living megaherbivore taxa of similar body size (i.e. rhinoceroses, elephants) are hindgut fermenters (Clauss et al. 2003). The fermentative digestion of plant structural tissues in both foregut and hindgut fermenting herbivores is performed by commensal microbial floras (Stevens & Hume

1998). The hippo forestomach supports substantial microbial fermentation activity that facilitates the digestion of plant matter (Thurston et al. 1968, Thurston & Grain 1971, Arman & Field 1973, Thurston & Noiroth-Thimothée 1973, Van Hoven 1978, Clemens & Maloiy 1982, Ito et al. 2002). The multi-chambered forestomach of the hippo is distinctively different from those of other extant foregut fermenting ungulates (ruminants, camelids, and peccaries) and consists of a series of two blind sacs and a massive tubular chamber with ventral semilunar folds (Langer 1976, 1988). Several regions of the hippo forestomach are lined with a papillated epithelium similar to that of ruminants. Differences in the passage rates of fluids and particles in the hippo forestomach suggest that harvesting of microbial matter from the forestomach is particularly pronounced in hippos (Clauss et al. 2004, Müller et al. 2011). Like other foregut fermenters, the hippo has a forestomach 'groove' formed by muscular ridges and assumed to facilitate the bypass of milk during suckling, in order to avoid microbial fermentation of lactose in the forestomach (Langer 1988). The distal part of the gastrointestinal tract is simple, and the colon is short and undifferentiated with no caecum (Clemens & Maloiy 1982). One of the colon's functions is to re-absorb water from the digesta, so the short colon corresponds to the very watery nature of hippo faeces with a low dry matter content

of about 10% (Clemens & Maloiy 1982), and it has been speculated that such high faecal water losses are linked with the hippo's aquatic lifestyle where water is not important as a critical limiting resource (Clauss et al. 2003).

CARNIVORY IN HERBIVORES

The concept that an ungulate herbivore possessing a specialised digestive tract and co-evolved gut microflora adapted to the fermentation and digestion of plant materials would deliberately ingest animal tissues as food challenges our intuitive understanding of herbivore behaviour and digestive physiology. Nonetheless, there is a large body of literature that documents the deliberate ingestion of many types of animal tissues (including carrion, birds' eggs, fledgling birds, small mammals, and fish) by a wide range of ungulate taxa, including, but not limited to, antelopes, deer, and cattle (Denenberg et al. 1959, Dubost 1964, Abraham et al. 1977, Allan 1978, Case & McCullough 1987, Furness 1988, Pietz & Granfors 2000, Nack & Ribic 2005, Anonymous 2008, González-Redondo & Zamora-Lozano 2008, Squibb 2008, Hart 2013). Furthermore, the females of most mammals, including ungulate herbivores, normally ingest their placental tissues after giving birth (placentophagia; Kristal 1980). The primary exceptions to the rule are those mammals that give birth in water, i.e. cetaceans (Cetacea: whales, porpoises, and dolphins) and sirenians (Sirenia: manatees, dugongs; Kristal et al. 2012). It is not clear from the available literature whether hippos, which frequently, but not always, give birth in water, exhibit placentophagia behaviour.

All extant ruminants and foregut fermenters possess anatomical structures to divert milk from the developing fore-stomach (Langer 1988), because the fermentation of lactose can result in acidosis, maldigestion, malabsorption, and possible death (Breukink et al. 1988). However, other types of animal matter (muscle, gut tissues, blood, bone, etc.) do not contain the high levels of lactose and other easily fermentable carbohydrates present in milk and do not induce the same types of digestive dysfunction. Studies have demonstrated that feed supplements containing meat-and-bone meal, blood meal, and other animal tissue by-products can significantly improve the growth performance of domestic cattle, sheep, and other ruminants (Loerch et al. 1983, Clark et al. 1987). The once-widespread practice of feeding such supplements to domestic ruminants was only banned in various countries when the practice was identified as being responsible for the emergence and transmission of bovine spongiform encephalopathy (BSE) in cattle and linked to Creutzfeldt–Jakob disease in humans that consumed potentially BSE-infected tissues from infected cattle (Scott et al. 1999, Prince et al. 2003). It should also not be overlooked that cetaceans, close relatives of hippos and strict carnivores, also possess complex forestomachs that support an active

fermenting gut microbiome in representatives of the baleen whales (Herwig et al. 1984, Olsen et al. 1994, Olsen & Mathiesen 1996).

Taken together, this body of evidence suggests that opportunistic carnivory could be a widespread trait among mammalian herbivore species and that most mammalian herbivores can and do consume a certain amount of animal prey when it is available in a form that they can ingest without undue difficulty. According to this hypothesis, the general absence of carnivory by herbivores may not be due to constraints imposed by their digestive physiology, but rather due to biomechanical limitations in their ability to secure or ingest animal tissues (or both). Disease transmission and avoidance may be a selective factor modulating the prevalence of carnivory by ungulates, however, as carnivory may lead to exposure to disease pathogens not normally associated with herbivory. Due to its large body size and unusual mouth and dental configurations, the hippo may represent an extreme case in which the predation and scavenging of large mammals by an ungulate species is not constrained by biomechanical factors and is facilitated by an existing tendency for highly aggressive agonistic and territorial behaviour towards conspecifics and other large vertebrates.

ANTHRAX IN HIPPOS

Anthrax is a potentially fatal disease caused by the bacterium *Bacillus anthracis*. Anthrax is one of the most widely distributed of all zoonotic diseases, and no other infectious disease is known to affect such a wide range of mammalian species, including humans (Beyer & Turnbull 2009). Anthrax is found on most continents, occurring at elevations from sea level to up to 4000 m, in biomes ranging from the subarctic taiga regions of Eurasia and North America southward into the humid and arid tropics of Asia, Africa, South America, Australia, New Guinea, and the Caribbean islands (Hughes-Jones 1999, Gainer & Oksanen 2012). Vaccination of livestock has greatly reduced the incidence of anthrax in many historically endemic areas, but sporadic outbreaks among wildlife and unvaccinated livestock are still a problem in many areas of the world (Hughes-Jones 1999).

All mammals and some species of birds are susceptible to anthrax infections, although high levels of anthrax mortality during outbreaks are most frequently associated with large herbivores and ungulates (e.g. cattle, deer, antelopes, bison, zebras, elephants, and hippos). A recent study from the Etosha National Park in Namibia indicates that sub-lethal anthrax infections among zebras and certain other ungulate species may be more common than has been recognised in the past (Cizauskas et al. 2014). Ruminant ungulates are typically the most susceptible species, with anthrax causing major mortality among livestock and

wildlife populations worldwide, whereas mammalian carnivores, swine, and vultures tend to have relatively high levels of resistance to anthrax infections (Beyer & Turnbull 2009, Bengis & Frean 2014).

Anthrax infections can occur from exposure through skin contact, ingestion, inhalation, or insect vectors (biting flies and blowflies); infections acquired through ingestion and inhalation routes are typically associated with higher rates of mortality than cutaneous infections (Turnbull 2008). Carnivores typically contract gastrointestinal or oropharyngeal anthrax by feeding on infected animals. Humans most commonly contract anthrax via cutaneous infection when handling infected animals or carcasses, meat, hides, wool, or bones of infected animals, inhalation of spores from wool or animal hides, and more rarely by eating meat from infected animals (Beyer & Turnbull 2009).

Most anthrax infections in herbivores are believed to occur from the ingestion or inhalation of spores from contaminated forage or soils (Hugh-Jones & De Vos 2002, Fasanella et al. 2014). Hippos and other grazing herbivores may ingest spores in soil particles while grazing on short grasses, or by direct consumption of contaminated soils at mineral licks (Viljoen et al. 1928, Mapesa et al. 2008, Turner et al. 2013, Havarua et al. 2014). Animals grazing over dry, dusty, and contaminated soil can also inhale spores, and respiratory anthrax has been reported in cattle (Beyer & Turnbull 2009). Contamination of plant forage by anthrax spores regurgitated by necrophagous flies (blowflies: Calliphoridae) that have been feeding on the carcasses of anthrax-killed animals is an important driver of mass anthrax outbreaks among browsing ungulates such as African antelopes (impala, kudu, sable antelope *Hippotragus niger*) and American white-tailed deer *Odocoileus virginianus* (Braack & de Vos 1990, Hughes-Jones 1999, Blackburn et al. 2010, Bengis & Frean 2014). Haemophagous biting flies, including stable flies (Muscidae: *Stomoxys*) and horse flies (Tabanidae), can have a significant role in the long-distance dispersal and proliferation of anthrax outbreaks among livestock and wild ungulates in Africa and North America (Turell & Knudson 1987, de Vos & Turnbull 2004, Hugh-Jones & Blackburn 2009, Blackburn et al. 2014, Fasanella et al. 2014).

Although it is possible that gastrointestinal infections could occur through drinking of water contaminated with anthrax spores or bacteria, there is little available evidence to demonstrate that wild mammals frequently acquire fatal gastrointestinal infections through this mechanism (Hugh-Jones & De Vos 2002, Cizauskas et al. 2014). However, the apparent low colonic water reabsorption capability of hippos (Clauss et al. 2003) may increase drinking water requirements, and the high levels of water contamination from hippo carcasses (Fig. 2) could increase their susceptibility to infection via this route. The antibacterial properties of hippo subdermal gland

secretions (Hashimoto et al. 2007, Galasso & Pichierri 2009), on the other hand, could limit the susceptibility of hippos to cutaneous anthrax infections from contaminated water. In summary, hippos may be peculiar among susceptible herbivores in having increased susceptibility to anthrax exposure from carnivory, scavenging behaviour, and consumption of contaminated water.

Mortality rates from anthrax infections are modulated by the type of exposure, level of exposure, type of infection (cutaneous, gastrointestinal, and respiratory), and by species-specific variations in susceptibility and immunity (Hugh-Jones & De Vos 2002). Within any given area, anthrax outbreaks often affect one species more than others; other susceptible species in that area may be only marginally affected. This phenomenon has usually been attributed to ecological and behavioural factors, but strain differences may also be involved (Beyer & Turnbull 2009).

The life cycle of *Bacillus anthracis* is markedly different from that of most other pathogenic bacteria, in that its replication and persistence are associated with extreme virulence and rapid death of the host, followed by an extended period of dormancy within the environment in a sporulated form (Bengis & Frean 2014). Upon entry into a susceptible host, *Bacillus anthracis* spores germinate into rapidly reproducing vegetative cells that produce toxins. Vegetative cells produce environmentally resilient and metabolically dormant spores, which are resistant to desiccation. Sporulation does not occur at temperatures below 9 °C (Beyer & Turnbull 2009), and the mechanisms that trigger sporulation in *Bacillus anthracis* vegetative cells in host tissues are poorly understood, although exposure of bodily fluids to air following host death apparently helps trigger sporulation (Hugh-Jones & De Vos 2002, Bellan et al. 2013).

Viable *Bacillus anthracis* spores can persist in the environment for many years; viable anthrax spores were recovered from bone collected at an archaeological site in South Africa estimated to be at least 200 years old (de Vos 1990). Anthrax spores exhibit their highest rates of survival in alkaline soils with relatively high calcium and organic matter content (Bengis & Frean 2014). Recent experimental research indicates that *Bacillus anthracis* may have mycorrhizae-like symbiotic relationships with the roots of certain grass species that can promote plant growth, independently of any organic matter fertilisation effect from contaminated blood or carcasses (Ganz et al. 2014).

Anthrax outbreaks in African wildlife may result in the death of 10–90% of the populations of affected ungulate species within outbreak areas (Viljoen et al. 1928, Pienaar 1961, Prins & Weyerhaeuser 1987, Lindeque & Turnbull 1994, Clegg et al. 2007, Muoria et al. 2007, Lembo et al. 2011). Mass anthrax outbreaks in hippo populations tend to be associated with late dry season periods or drought conditions, when hippos are concentrated in high densities within

river channels and lakes where perennial surface water is available. However, hippo mortalities from anthrax have also been reported during rainy seasons (Turnbull et al. 1991, Mapesa et al. 2008, Hampson et al. 2011).

Anthrax outbreaks involving the deaths of thousands of hippos, with estimated population mortality rates of 15–20%, have been reported from the Rift Valley Lakes region in Uganda and the Luangwa River Valley in Zambia (Kingdon 1982, Turnbull et al. 1991, Mapesa et al. 2008). An exceptionally large and protracted anthrax outbreak among hippos in Queen Elizabeth National Park (QENP), Uganda, during 2004 and 2005 resulted in the deaths of approximately 15% of the resident hippo population (Mapesa et al. 2008, Coffin et al. 2015). Media reports indicate that there were at least 10 human anthrax cases linked to this outbreak (Anonymous 2004). Other significant episodes of hippo mortality from anthrax are reported to have occurred in QENP in 1937, 1959, 1962 and 1991 (Kingdon 1982, Mapesa et al. 2008). The 2004/2005 anthrax outbreak in QENP was particularly notable in that it appeared to be largely restricted to hippos; very few wild mammals of other species were affected (Mapesa et al. 2008; Fig. 4). The spatial and temporal distribution of hippo anthrax mortality during the 2004/2005 outbreak indicates that the outbreak progressed in an upstream-to-downstream direction from Lake George to Lake Edward through the Kazinga Channel, a pattern consistent with the hypothesis that the outbreak spread was associated with the downstream dispersal of the floating carcasses of anthrax-killed hippos. During a field investigation of the 2004/2005 QENP anthrax outbreak, Leendertz (this study) observed a hippo feeding on the extruded intestines of an anthrax-killed hippo carcass, and it appears possible that the proliferation of the anthrax outbreak among hippos at this site may have been exacerbated by hippos feeding on anthrax-infected tissues from the carcasses of dead hippos.

Anthrax is considered hyperendemic in the semi-arid savanna regions of Zambia. The highest prevalence of outbreaks occurs in the Luangwa River Valley of eastern Zambia and the upper Zambezi River floodplain region of western Zambia. Human cases occur frequently in conjunction with outbreaks in livestock and wildlife in Zambia, from the handling and butchering or consumption of meat from infected carcasses (Hang'ombe et al. 2012, Munang'andu et al. 2012). A mass anthrax outbreak among hippos in the Luangwa Valley of Zambia during June–November 1987 may have killed more than 4000 hippos, as much as 21% of the resident hippo population (Turnbull et al. 1991). The initial outbreak in South Luangwa National Park during 1987 was followed by another outbreak among hippos approximately 100 km upstream in the North Luangwa National Park and the Musalangu Game Management Area during 1988 (Turnbull et al. 1991, Siamudaala

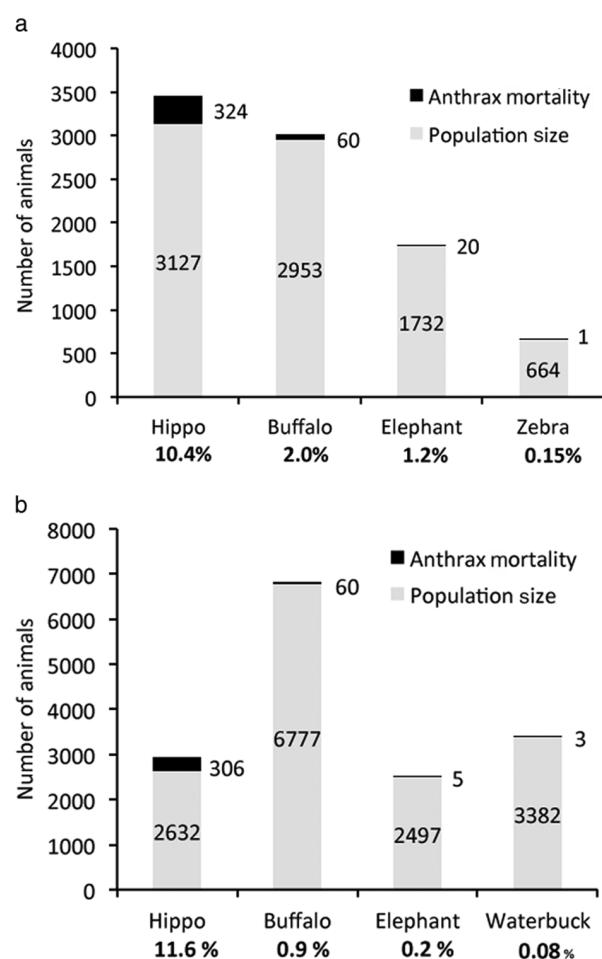


Fig. 4. Anthrax mortality reported in hippos *Hippopotamus amphibius*, buffalo *Syncerus caffer*, elephants *Loxodonta africana*, zebras *Equus burchelli*, and waterbuck *Kobus ellipsiprymnus* (a) in the central Luangwa Valley, Zambia, during 1987 (data from Siamudaala 2005) and (b) in Queen Elizabeth National Park, Uganda, during 2004–2005 (data from Mapesa et al. 2008). Mortality is expressed as a percentage of the population size under each bar.

2005). The vast majority of anthrax mortality among wildlife species during the 1987–1988 outbreak occurred in hippos; relatively few individuals of other ungulate species were reported to have died (Fig. 4ab).

At least 85 hippos died during another anthrax outbreak in the Luangwa River in August–September 2011. *Bacillus anthracis* was isolated from dried and smoked hippo meat confiscated from local residents, and no other species of wildlife or livestock were known to have been affected (Hang'ombe et al. 2012). A total of 511 human cases, including at least five deaths, were linked to handling or consumption of meat from hippo carcasses during the 2011 outbreak (Anonymous 2011, 2012a). Hippos were observed feeding on

carcasses of dead hippos on several occasions in widely separated locations during this outbreak (Hang'ombe, this study), and we hypothesise that this same behaviour may have been a key factor in the mass hippo mortality observed during the 1987–1988 outbreak (Figs 2 and 4).

Anthrax outbreaks in South Africa's Kruger National Park (KNP) are seldom associated with mass mortality among hippos on the scale reported from Zambia and Uganda, although sporadic anthrax mortality of hippos has been reported (Pienaar 1961, de Vos 1990, de Vos & Bryden 1995). Major outbreaks occurred in 1959–1960, 1970, 1990–1991, 1993, and 1999 (Bengis et al. 2003). Highest rates of mortality from anthrax outbreaks in KNP tend to occur among African buffalo and browsing antelope species such as kudu, nyala *Tragelaphus angasii*, sable antelope, and roan antelope *Hippotragus equinus*. Gastrointestinal anthrax from the consumption of leaves contaminated by anthrax spores regurgitated by blowflies that have fed on the carcasses of infected animals appears to play a dominant role in the epidemiology of anthrax outbreaks among ungulates within the KNP, and outbreaks within KNP usually cease following the onset of the rainy season (de Vos 1990, Bengis et al. 2003). At least 18 hippos in the Letaba River of KNP were suspected to have died from anthrax at the end of the 1990 dry season, followed by another seven suspected anthrax hippo mortalities during the 1991/1992 drought, or approximately 4% of an estimated total population of 650 hippos (Viljoen & Biggs 1998). At least 30 hippos were reported to have died from anthrax in the Letaba and Olifants River areas of KNP during a two-week period in October 2012, late in the course of an extended anthrax outbreak that killed nearly 50% of the KNP roan antelope population between August and November 2012 (Anonymous 2012b, c). Carnivory by hippos may be a contributing factor to anthrax mortality among hippos in the KNP, given that Dorward (2015) observed and photographed an adult hippo feeding on the carcass of a dead adult hippo in April 2014.

Hippos, and also pygmy hippos, could play an important role in the epidemiology of anthrax and other diseases in tropical rainforest landscapes of West Africa and the Congo Basin. Hippos and pygmy hippos could be susceptible to infection with the novel type of forest anthrax caused by *Bacillus cereus* biovar *anthracis*, which has been documented from chimpanzees *Pan troglodytes* in the Ivory Coast and gorillas *Gorilla gorilla* in Cameroon (Klee et al. 2006). Very little is currently known about hippo populations in rainforest habitats of the Congo Basin region, or about the behaviour and ecology of pygmy hippos in the Guinean rainforest region of West Africa (Hentschel 1990, Nchanji & Fotso 2006, Mallon et al. 2011). Although no disease-related deaths of pygmy hippos have been identified in more than 15 years of intensive wildlife monitoring in Tai National Park, Ivory Coast (Calvignac-Spencer et al. 2012), pygmy

hippos occur at low densities and are solitary in their habits, and the detection and identification of carcasses is much more difficult in tropical rainforests than in savanna habitats (Rouquet et al. 2005).

CONCLUSIONS

Mass anthrax outbreaks in hippo populations can occur in the absence of evident contemporaneous anthrax mortality among other anthrax-susceptible herbivore species within the same habitat, or asynchronously and at orders-of-magnitude higher levels than that recorded among elephants, buffalo, and other anthrax-susceptible ungulate species within their habitats. We hypothesise that the observed anomalies associated with mass anthrax outbreaks among hippos can be attributed, at least in part, to carnivory and scavenging of anthrax-infected animal carcasses by hippos, including, but not limited to, those of dead hippos.

The available data indicate that carnivory by hippos is an inherent dimension of their fundamental ecological niche. The available data do not allow us to identify factors contributing to the expression of carnivory, as the behaviour was observed in different situations. Carnivory by hippos has been observed during droughts with putative nutritional stress, and also in situations of superabundant opportunistic resources, such as during mass anthrax outbreaks in hippos or mass drowning of wildebeest crossing the Mara River. Further observational studies and field experiments should be conducted to evaluate the behavioural response of hippos at different sites to the presence of nearby animal carcasses, and whether such a response varies seasonally. Additionally, the use of stable isotope analyses should be investigated. Such analysis could help us to identify the contribution of animal tissues to hippo diets, as has been done in chimpanzees (Fahy et al. 2013), in order to test whether carnivory in hippos has a nutritional relevance beyond an increased likelihood of anthrax infection.

Our hypothesis that carnivory and scavenging by hippos may serve as a principal driver for mass anthrax outbreaks in hippo populations has important implications for the management of anthrax outbreaks. The findings of this review indicate that the standard practice of burying or burning suspected anthrax-infected animal carcasses may be especially effective for the control of mass anthrax outbreaks in hippo populations, and that the effect of this measure should be scientifically evaluated.

ACKNOWLEDGEMENTS

The authors are indebted to many individuals for their contributions to the genesis of this study, including Thure Cerling, Christopher Dutton, Keith Eltringham, Martin Hugh-Jones, Rebecca Lewison, Peter Steyn, Peter Turnbull,

and John Woodford. Funding for research in the Mara River was provided by the U.S. National Science Foundation (DEB 1354053 and 1354062).

REFERENCES

- Abraham KF, Mineau P, Cooke F (1977) Unusual predators of snow goose eggs. *Canadian Field-Naturalist* 91: 317–318.
- Allan TA (1978) Further evidence of white-tailed deer eating birds in mist nets. *Bird Banding* 49: 184.
- Anonymous (2004) Anthrax, hippopotamus, human – Uganda. International Society for Infectious Diseases, ProMed-mail post Archive Number: 20041109.3027.
- Anonymous (2008) Carnivorous behavior patterns in deer. In *Report of the Committee on Wildlife Diseases*, 3–4. United States Animal Health Association, Saint Joseph, Missouri, USA.
- Anonymous (2011) Zambia: Anthrax outbreak (situation as of September 4, 2011). World Health Organization, Geneva, Switzerland.
- Anonymous (2012a) Annual Report for Zambia Country Office 2011. World Health Organization, Geneva, Switzerland.
- Anonymous (2012b) Anthrax outbreak in the north of the KNP. Kruger National Park. <http://www.krugerpark.co.za/kruger-park-news-anthrax-outbreak-north-knp-25573.html>
- Anonymous (2012c) Anthrax outbreak affects hippos in the Kruger National Park. South African National Parks Boards Media Release. <http://www.sanparks.org/about/news/?id=55360>
- Arman P, Field CR (1973) Digestion in the hippopotamus. *East African Wildlife Journal* 11: 9–17.
- Bekker JL, Hoffman LC, Jooste PJ (2012) Wildlife-associated zoonotic diseases in some southern African countries in relation to game meat safety: a review. *Onderstepoort Journal of Veterinary Research* 79: E1–E12.
- Bellan SE, Turnbull PCB, Beyer W, Getz WM (2013) Effects of experimental exclusion of scavengers from carcasses of anthrax-infected herbivores on *Bacillus anthracis* sporulation, survival, and distribution. *Applied and Environmental Microbiology* 79: 3756–3761.
- Bengis RG, Erasmus JM (1988) Wildlife diseases in South Africa: a review. *Revue Scientifique et Technique Office International des Epizooties* 7: 807–821.
- Bengis RG, Frean J (2014) Anthrax as an example of the One Health concept. *Revue Scientifique Et Technique-Office International Des Epizooties* 33: 593–604.
- Bengis RG, Kock RA, Fischer J (2002) Infectious animal diseases: the wildlife/livestock interface. *Revue Scientifique et Technique Office International des Epizooties* 21: 53–65.
- Bengis RG, Grant R, de Vos V (2003) *Wildlife Diseases and Veterinary Controls: A Savanna Ecosystem Perspective*. Island Press, Washington, D.C., USA.
- Beyer W, Turnbull PCB (2009) Anthrax in animals. *Molecular Aspects of Medicine* 30: 481–489.
- Blackburn JK, Curtis A, Hadfield TL, O’Shea B, Mitchell MA, Hugh-Jones ME (2010) Confirmation of *Bacillus anthracis* from flesh-eating flies collected during a west Texas anthrax season. *Journal of Wildlife Diseases* 46: 918–922.
- Blackburn JK, Van Ert M, Mullins JC, Hadfield TL, Hugh-Jones ME (2014) The necrophagous fly anthrax transmission pathway: empirical and genetic evidence from wildlife epizootics. *Vector-Borne and Zoonotic Diseases* 14: 576–583.
- Boissier JR, Zazzo A, Merceron G, Blondel U, Vignaud P, Likius A et al. (2005) Diets of modern and late Miocene hippopotamids: evidence from carbon isotope composition and micro-wear of tooth enamel. *Palaeogeography, Palaeoclimatology, Palaeoecology* 221: 153–174.
- Braack LEO, de Vos V (1990) Feeding habits and flight range of blow-flies (*Chrysomya* spp.) in relation to anthrax transmission in the Kruger National Park, South Africa. *Onderstepoort Journal of Veterinary Research* 57: 141–142.
- Breukink HJ, Wensing T, Buisman AV, Vanbruinessenkapenberg EG, Devisser N (1988) Consequences of failure of the reticular groove reflex in veal calves fed milk replacer. *Veterinary Quarterly* 10: 126–135.
- Calvignac-Spencer S, Leendertz SA, Gillespie TR, Leendertz FH (2012) Wild great apes as sentinels and sources of infectious disease. *Clinical Microbiology and Infection* 18: 521–527.
- Case DJ, McCullough DR (1987) White-tailed deer forage on alewives. *Journal of Mammalogy* 68: 195–197.
- Cerling TE, Harris JM, Hart JA, Kaleme P, Klingel H, Leakey MG et al. (2008) Stable isotope ecology of the common hippopotamus. *Journal of Zoology* 276: 204–212.
- Cizauskas CA, Bellan SE, Turner WC, Vance RE, Getz WM (2014) Frequent and seasonally variable sublethal anthrax infections are accompanied by short-lived immunity in an endemic system. *Journal of Animal Ecology* 83: 1078–1090.
- Clark JH, Murphy MR, Crooker BA (1987) Supplying the protein needs of dairy cattle from by-product feeds. *Journal of Dairy Science* 70: 1092–1109.
- Clauss M, Frey R, Kiefer B, Lechner-Doll M, Loehlein W, Polster C et al. (2003) The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters. *Oecologia* 136: 14–27.
- Clauss M, Schwarm A, Ortmann S, Alber D, Flach EJ, Kuhne R et al. (2004) Intake, ingesta retention, particle size distribution and digestibility in the Hippopotamidae. *Comparative Biochemistry and Physiology A* 139: 449–459.
- Clauss M, Streich WJ, Schwarm A, Ortmann S, Hummel J (2007) The relationship of food intake and ingesta passage predicts feeding ecology in two different megaherbivore groups. *Oikos* 116: 209–216.
- Clegg SB, Turnbull PCB, Foggin CM, Lindeque RM (2007) Massive outbreak of anthrax in wildlife in the Malilangwe Wildlife Reserve, Zimbabwe. *Veterinary Record* 160: 113–118.

- Clemens ET, Maloiy GMO (1982) The digestive physiology of three East African herbivores – the elephant, rhinoceros and hippopotamus. *Journal of Zoology* 198: 141–156.
- Coffin JL, Monje F, Asiiimwe-Karimu G, Amuguni HJ, Odoch T (2015) A One Health, participatory epidemiology assessment of anthrax (*Bacillus anthracis*) management in Western Uganda. *Social Science & Medicine* 129: 44–50.
- Cowan DF, Thurlbeck WM, Laws RM (1967) Some diseases of the hippopotamus in Uganda. *Pathologia Veterinaria* 4: 552–567.
- Crowther R, Whyte I (1989) Hippos interfere. *Custos* 18: 10.
- de Longh HH, de Jong CB, van Goethem J, Klop E, Brunsting AMH, Loth PE et al. (2011) Resource partitioning among African savanna herbivores in North Cameroon: the importance of diet composition, food quality and body mass. *Journal of Tropical Ecology* 27: 503–513.
- de Vos V (1990) The ecology of anthrax in the Kruger National Park. *Salisbury Medical Bulletin* 68: 19–23.
- de Vos V, Bryden HB (1995) Anthrax in the Kruger National Park: temporal and spatial patterns of disease occurrence. *Salisbury Medical Bulletin* 87: 26–30.
- de Vos V, de Klerk BD (1980) Tetanus in a free-living hippopotamus (*Hippopotamus amphibius capensis*) from the Kruger National Park. *Koedoe* 23: 171–175.
- de Vos V, Turnbull PCB (2004) Anthrax. In: Coetzer JAW, Tustin RC (eds) *Infectious Diseases of Livestock, with Special Reference to Southern Africa*, 1788–1818. Oxford University Press, Cape Town, South Africa.
- Denenberg VH, Petropolis SF, Sawin PB, Ross S (1959) Genetic, physiological, and behavioral background of reproduction in the rabbit: VI. Maternal behavior with reference to scattered and cannibalized newborn and mortality. *Behaviour* 15: 71–76.
- Despres L, Kruger FJ, Imbert Establet D, Adamson ML (1995) ITS2 ribosomal RNA indicates *Schistosoma hippopotami* is a distinct species. *International Journal for Parasitology* 25: 1509–1514.
- Dorward LJ (2015) New record of cannibalism in the common hippo, *Hippopotamus amphibius* (Linnaeus, 1758). *African Journal of Ecology* 53: 385–387.
- Dubost G (1964) Un ruminant à régime alimentaire partiellement carni: le chevrotaine aquatique (*Hyaemoschus aquaticus* Ogilby). *Biologia Gabonica* 1: 21–23.
- Dudley JP (1996) Record of carnivory, scavenging and predation for *Hippopotamus amphibius* in Hwange National Park, Zimbabwe. *Mammalia* 60: 486–488.
- Dudley JP (1998) Reports of carnivory by the common hippo *Hippopotamus amphibius*. *South African Journal of Wildlife Research* 28: 58–59.
- Dunham KM (1990) Fruit production by *Acacia albida* trees in Zambezi riverine woodlands. *Journal of Tropical Ecology* 6: 445–457.
- Dutton CL, Subalusky AL (2011) Flesh-eating hippos sighted in the Maasai Mara. *SWARA, Journal of the East African Wildlife Society* 11: 54–55.
- Ellery WN, Dahlberg AC, Strydom R, Neal MJ, Jackson J (2003) Diversion of water flow from a floodplain wetland stream: an analysis of geomorphological setting and hydrological and ecological consequences. *Journal of Environmental Management* 68: 51–71.
- Eltringham S (1999) *The Hippos: Natural History and Conservation*. Academic Press, London, UK.
- Fahy GE, Richards M, Riedel J, Hublin JJ, Boesch C (2013) Stable isotope evidence of meat eating and hunting specialization in adult male chimpanzees. *Proceedings of the National Academy of Sciences* 110: 5829–5833.
- Fasanella A, Adone R, Hugh-Jones M (2014) Classification and management of animal anthrax outbreaks based on the source of infection. *Annali Dell Istituto Superiore Di Sanita* 50: 192–195.
- Field CR (1970) A study of the feeding habits of the hippopotamus (*Hippopotamus amphibius* Linn.) in the Queen Elizabeth National Park, Uganda, with some management implications. *Zoologica Africana* 5: 71–86.
- Fritz J, Hummel J, Kienzle E, Arnold C, Nunn C, Clauss M (2009) Comparative chewing efficiency in mammalian herbivores. *Oikos* 118: 1623–1632.
- Frost J (1996) *A Survey of the Hippopotamus in Captivity in the British Isles*. North of England Zoological Society, Chester, UK.
- Furness RW (1988) Predation on ground-nesting seabirds by island populations of red deer (*Cervus elaphus*) and sheep (*Ovis*). *Journal of Zoology* 216: 565–573.
- Gainer R, Oksanen A (2012) Anthrax and the Taiga. *Canadian Veterinary Journal-Revue Veterinaire Canadienne* 53: 1123–1125.
- Galasso V, Pichieri F (2009) Probing the molecular and electronic structure of norhipposudoric and hipposudoric acids from the red sweat of *Hippopotamus amphibius*: a DFT investigation. *Journal of Physical Chemistry A* 113: 2534–2543.
- Ganz HH, Turner WC, Brodie EL, Kusters M, Shi Y, Sibanda H et al. (2014) Interactions between *Bacillus anthracis* and plants may promote anthrax transmission. *PLoS Neglected Tropical Diseases* 8: e2903.
- Garnham PCC (1960) Blood parasites of hippopotamus in Uganda. *East African Medical Journal* 37: 495.
- González-Redondo P, Zamora-Lozano M (2008) Neonatal cannibalism in cage-bred wild rabbits (*Oryctolagus cuniculus*). *Archivos de Medicina Veterinaria* 40: 281–287.
- Grey J, Harper DM (2002) Using stable isotope analyses to identify allochthonous inputs to Lake Naivasha mediated via the hippopotamus gut. *Isotopes in Environmental and Health Studies* 38: 245–250.
- Hampson K, Lembo T, Bessell P, Auty H, Packer C, Halliday J et al. (2011) Predictability of anthrax infection in the Serengeti, Tanzania. *Journal of Applied Ecology* 48: 1333–1344.
- Hang'ombe MB, Mwansa JCL, Muwowa S, Mulenga P, Kapina M, Musenga E et al. (2012) Human-animal anthrax outbreak in the Luangwa valley of Zambia in 2011. *Tropical Doctor* 42: 136–139.

- Hart J (2013) *Hyemoschus aquaticus* Water Chevrotain. In: Kingdon J, Hoffman M (eds) *Mammals of Africa: Pigs, Hippopotamuses, Chevrotain, Giraffes, Deer and Bovids*, 88–94. Bloomsbury Academic, London, UK.
- Hashimoto K, Saikawa Y, Nakata M (2007) Studies on the red sweat of the *Hippopotamus amphibius*. *Pure and Applied Chemistry* 79: 507–517.
- Havarua Z, Turner WC, Mfune JK (2014) Seasonal variation in foraging behaviour of plains zebra (*Equus quagga*) may alter contact with the anthrax bacterium (*Bacillus anthracis*). *Canadian Journal of Zoology* 92: 331–337.
- Heckel ME (1879) Trichinosis in a young hippopotamus. *Journal of the Royal Microscopical Society* 2: 571–572.
- Hentschel K (1990) *Untersuchungen zu Status, Ökologie und Erhaltung des Zwerghflusspferdes (Choeropsis liberiensis)*. Technische Universität Carolo-Wilhelmina, Braunschweig, Germany.
- Herring SW, Herring SE (1974) Superficial masseter and gape in mammals. *American Naturalist* 108: 561–576.
- Herwig RP, Staley JT, Nerini MK, Braham HW (1984) Baleen whales: preliminary evidence for forestomach microbial fermentation. *Applied and Environmental Microbiology* 47: 421–423.
- Hugh-Jones M, Blackburn J (2009) The ecology of *Bacillus anthracis*. *Molecular Aspects of Medicine* 30: 356–367.
- Hugh-Jones MH, De Vos V (2002) Anthrax in wildlife. *Revue Scientifique et Technique (International Office of Epizootics)* 21: 359–383.
- Hughes-Jones M (1999) 1996–97 global anthrax report. *Journal of Applied Microbiology* 87: 189–191.
- Ito A, Miyazaki Y, Imai S (2002) Descriptions of new Parentodinium ciliates in the family Parentodiniidae n. fam. from *Hippopotamus amphibius* in comparison with some entodiniomorphs from horses and cattle. *European Journal of Protistology* 37: 405–426.
- Kanga EM, Ongut JO, Piepho H-P, Olff H (2013) Hippopotamus and livestock grazing: influences on riparian vegetation and facilitation of other herbivores in the Mara Region of Kenya. *Landscape and Ecological Engineering* 9: 47–58.
- Karstad EL, Hudson RJ (1986) Social organization and communication of riverine hippopotami in southwestern Kenya. *Mammalia* 50: 153–164.
- Kingdon J (1982) *East African Mammals*. University of Chicago Press, Chicago, USA.
- Klee SR, Ozel M, Appel B, Boesch C, Ellerbroek H, Jacob D et al. (2006) Characterization of *Bacillus anthracis*-like bacteria isolated from wild great apes from Côte d'Ivoire and Cameroon. *Journal of Bacteriology* 188: 5333–5344.
- Kristal MB (1980) Placentophagia – a biobehavioral enigma – or de gustibus non disputandum est. *Neuroscience and Biobehavioral Reviews* 4: 141–150.
- Kristal MB, DiPirro JM, Thompson AC (2012) Placentophagia in humans and nonhuman mammals: causes and consequences. *Ecology of Food and Nutrition* 51: 177–197.
- Langer P (1976) Functional anatomy of stomach of *Hippopotamus amphibius* L. 1758. *South African Journal of Science* 72: 12–16.
- Langer P (1988) *The Mammalian Herbivore Stomach. Comparative Anatomy, Function and Evolution*. Gustav Fischer Verlag, Stuttgart, Germany.
- Laws RM (1968) Dentition and ageing of the hippopotamus. *East African Wildlife Journal* 6: 19–52.
- Lembo T, Hampson K, Auty H, Beesley CA, Bessell P, Packer C et al. (2011) Serologic surveillance of anthrax in the Serengeti Ecosystem, Tanzania, 1996–2009. *Emerging Infectious Diseases* 17: 387–394.
- Lewison R (1998) Infanticide in the hippopotamus: evidence for polygynous ungulates. *Ethology Ecology & Evolution* 10: 277–286.
- Lindeque PM, Turnbull PCB (1994) Ecology and epidemiology of anthrax in the Etosha National Park, Namibia. *Onderstepoort Journal of Veterinary Research* 61: 71–83.
- Lock JM (1972) Effects of hippopotamus grazing on grasslands. *Journal of Ecology* 60: 445–467.
- Loerch SC, Berger LL, Plegge SD, Fahey GC (1983) Digestibility and rumen escape of soybean meal, blood meal, meat and bone meal and dehydrated alfalfa nitrogen. *Journal of Animal Science* 57: 1037–1047.
- Mallon D, Wightman C, De Ornellas P, Collen B, Ransom C (2011) *Conservation Strategy for the Pygmy Hippopotamus*. IUCN Species Survival Commission, Gland, Switzerland.
- Mapesa MW, Atimnedi P, Tumwesige C (2008) Managing the 2004/05 anthrax outbreak in Queen Elizabeth and Lake Mburo National Parks, Uganda. *African Journal of Ecology* 46: 24–31.
- Michez A, Doucet J-L, Dendoncker N, Bouche P, Vermeulen C (2013) Preliminary description of the diet of *Hippopotamus amphibius* L. in Loango National Park (Gabon). *Biotechnologie Agronomie Société Et Environnement* 17: 580–583.
- Mugangu TE, Hunter ML (1992) Aquatic foraging by hippopotamus in Zaïre: response to a food shortage? *Mammalia* 56: 345–350.
- Munang'andu HM, Banda F, Siamudaala VM, Munyeme M, Kasanga CJ, Hamududu B (2012) The effect of seasonal variation on anthrax epidemiology in the upper Zambezi floodplain of western Zambia. *Journal of Veterinary Science* 13: 293–298.
- Muoria PK, Muruthi P, Kariuki WK, Hassan BA, Mijele D, Oguge NO (2007) Anthrax outbreak among Grevy's zebra (*Equus grevyi*) in Samburu, Kenya. *African Journal of Ecology* 45: 483–489.
- Müller DWH, Caton J, Codron D, Schwarm A, Lentle R, Streich WJ et al. (2011) Phylogenetic constraints on digesta separation: variation in fluid throughput in the digestive tract in mammalian herbivores. *Comparative Biochemistry and Physiology A* 160: 207–220.
- Nack JL, Ribic CA (2005) Apparent predation by cattle at grassland bird nests. *Wilson Bulletin* 117: 56–62.

- Nchanji AC, Foto RC (2006) Common hippopotamus (*Hippopotamus amphibius*): a survey on the River Djerem, Mbam-Djerem National Park, Cameroon. *Mammalia* 70: 9–13.
- Olivier RCD, Laurie WA (1974) Habitat utilization by hippopotamus in the Mara River. *African Journal of Ecology* 12: 249–271.
- Olsen MA, Mathiesen SD (1996) Production rates of volatile fatty acids in the minke whale (*Balaenoptera acutorostrata*) forestomach. *British Journal of Nutrition* 75: 21–31.
- Olsen MA, Aagnes TH, Mathiesen SD (1994) Digestion of herring by indigenous bacteria in the minke whale forestomach. *Applied and Environmental Microbiology* 60: 4445–4455.
- Owen-Smith RN (1988) *Megaherbivores – the Influence of Very Large Body Size on Ecology*. Cambridge University Press, Cambridge, UK.
- Pienaar UDV (1961) A second outbreak of anthrax amongst game animals in the Kruger National Park, 5th June to 11th October, 1960. *Koedoe* 4: 4–17.
- Pietz PJ, Granfors DA (2000) White-tailed deer (*Odocoileus virginianus*) predation on grassland songbird nestlings. *American Midland Naturalist* 144: 419–422.
- Plowright W, Laws RM, Tampton CS (1964) Serological evidence for the susceptibility of the hippopotamus (*Hippopotamus amphibius*) to natural infection with rinderpest virus. *Journal of Hygiene* 62: 329–336.
- Prince MJ, Bailey JA, Barrowman PR, Bishop KJ, Campbell GR, Wood JM (2003) Bovine spongiform encephalopathy. *Revue Scientifique et Technique de l'Office International des Epizooties* 22: 37–60.
- Prins HHT, Weyerhaeuser FJ (1987) Epidemics in populations of wild ruminants – anthrax and impala, rinderpest and buffalo in Lake Manyara National Park, Tanzania. *Oikos* 49: 28–38.
- Rouquet P, Froment JM, Bermejo M, Kilbourn A, Karesh W, Reed P et al. (2005) Wild animal mortality monitoring and human Ebola outbreaks, Gabon and Republic of Congo, 2001–2003. *Emerging Infectious Diseases* 11: 283–290.
- Schwarm A, Ortmann S, Hofer H, Streich WJ, Flach EJ, Kuhne R et al. (2006) Digestion studies in captive Hippopotamidae: a group of large ungulates with an unusually low metabolic rate. *Journal of Animal Physiology and Animal Nutrition* 90: 300–308.
- Scott MR, Will R, Ironside J, Nguyen HOB, Tremblay P, DeArmond SJ et al. (1999) Compelling transgenic evidence for transmission of bovine spongiform encephalopathy prions to humans. *Proceedings of the National Academy of Sciences of the United States of America* 96: 15137–15142.
- Siamudaala VM (2005) *A Study of the Epidemiology and Socio-Economic Impact of Anthrax in Luangwa Valley in Zambia*. University of Pretoria, Pretoria, South Africa.
- Squibb HW (2008) Carnivorous behavior patterns of deer: A preliminary investigation of the use of gut piles and carcasses by wildlife. In: *Report of the Committee on Wildlife Diseases*, 3–4. United States Animal Health Association, Saint Joseph, MO.
- Stevens CE, Hume ID (1998) Contributions of microbes in vertebrate gastrointestinal tract to production and conservation of nutrients. *Physiological Reviews* 78: 393–427.
- Steyn P (1999) Hippo carnivory. *Africa Environment and Wildlife* 7: 6–8.
- Subalusky AL, Dutton CL, Rosi-Marshall EJ, Post DM (2015) The hippopotamus conveyor belt: vectors of carbon and nutrients from terrestrial grasslands to aquatic systems in sub-Saharan Africa. *Freshwater Biology* 60: 512–525.
- Thomson GR, Bengis RG, Brown CC (2001) Picornavirus infections: foot-and-mouth disease. In: Williams ES, Barker IK (eds) *Infectious Diseases of Wild Animals*, 117–128. Iowa State Press, Ames, Iowa, USA.
- Thurston JP, Grain J (1971) Holotrich ciliates from the stomach of *Hippopotamus amphibius*, with descriptions of two new genera and four new species. *Journal of Protozoology* 18: 133–141.
- Thurston JP, Noiro-Timothée C (1973) Entodiniomorph ciliates from the stomach of *Hippopotamus amphibius* with descriptions of two new genera and three new species. *Journal of Protozoology* 20: 562–565.
- Thurston JP, Noiro-Timothée C, Arman P (1968) Fermentative digestion in the stomach of *Hippopotamus amphibius* and associated ciliate protozoa. *Nature* 218: 882–883.
- Turell MJ, Knudson GB (1987) Mechanical transmission of *Bacillus anthracis* by stable flies (*Stomoxys calcitrans*) and mosquitos (*Aedes aegypti* and *Aedes taeniorhynchus*). *Infection and Immunity* 55: 1859–1861.
- Turnbull PCB (2008) *Anthrax in Humans and Animals*, 4th ed. World Health Organization, Geneva, Switzerland.
- Turnbull PCB, Bell RHV, Saigawa K, Munyenjembe FEC, Mulenga CK, Makala LHC (1991) Anthrax in wildlife in the Luangwa Valley, Zambia. *Veterinary Record* 128: 399–403.
- Turner WC, Imologhome P, Havaria Z, Kaaya GP, Mfune JKE, Mpofu IDT et al. (2013) Soil ingestion, nutrition and the seasonality of anthrax in herbivores of Etosha National Park. *Ecosphere* 4: art13.
- Van Hoven W (1978) Digestive physiology in the stomach complex and hindgut of the hippopotamus. *South African Journal of Wildlife Research* 8: 59–64.
- Viljoen PC, Biggs HC (1998) Population trends of hippopotami in the rivers of the Kruger National Park, South Africa. In: Dunstone N, Gorman M (eds) *Behaviour and Ecology of Riparian Mammals*, 251–279. Clarendon Press, Oxford, UK.
- Viljoen PR, Curson HH, Fourie PJJ (1928) *Anthrax in South Africa with Special Reference to Improved Methods of Protective Inoculation*. Department of Agriculture, Pretoria, South Africa.
- Woodford J (2004) Anthrax, hippopotamus, human – Uganda. International Society for Infectious Diseases, ProMed-mail post Archive Number: 20041215.3317.