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LETTER TO THE EDITOR . . .

Epizootiology of Anthrax and Nyasa Wildebeest in the Selous Game Reserve, Tanzania

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The concepts many authorities have of anthrax epidemiology is that outbreaks of the peracute infection occur in certain areas where animals have had recent oral exposure to large numbers of spores (Blood et al., 1983, Veterinary Medicine, 6th Ed., Bailliere-Tindall, London, 1310 pp.). The extreme resistance of the spore form of *Bacillus anthracis* allows it to persist in the environment and thereby provide sources of infection. Schlingman et al., 1956, Am. J. Vet. Res. 17: 256–261) and Seto and Takizawa (1969, Natl. Inst. Anim. Health Q. (Tokyo) 9: 129–135) have demonstrated a relationship between the level of infection (sub-clinical to peracute) and the oral dose of spores; parenteral inoculations cause only sub-acute infections regardless of dose. In fact, the occurrence of the disease in Britain is associated with oral sources of large numbers of spores such as the feeding of bone meal or the ingestion of tannery effluent (Hugh-Jones and Hussaini, 1974, Vet. Rec. 94: 228–232).

In natural, undeveloped areas with free-ranging populations of wild animals and/or livestock of nomadic pastoralists, Minett (1952, Int. Off. Epizoot. Bull. 37: 238–300) associated outbreaks of anthrax with specific climatic and environmental conditions. Van Ness (1971, Science 172: 1303–1307) explained these outbreaks on the basis of the germination of spores in the environment and, depending on the nature of the environment, either the organism's multiplication and production of large numbers of spores or its elimination.

Minett (1950, J. Comp. Pathol. Ther. 60: 161–176) found that indeed spores did germinate and not persist in soils with nutrients and moisture, and that the disease often disappeared from areas when agriculture practices had been changed, but he also found that the non-spore form would not survive or reproduce in the soils of his experiments. In fact, its multiplication in non-animal media is the basis of the production of vaccines. In addition, a dose-dependent level of infection should mean a preponderance of sub-lethal infections throughout the entire period the animals are in the area rather than the periodic outbreaks of only the peracute infection. Furthermore, sub-lethal infections would mean older animals are more likely to have a resistance to the disease than young animals, the opposite of what is seen normally (Brunsdon, 1968, Vet. Rec. 82: 747–748). The explanation for outbreaks in natural anthrax areas is thus unclear.

The Miombo Research Center in the Selous Game Reserve, Tanzania, was established for studies of game management by the Danish Government. Early in the history of the Reserve, it was suspected that anthrax was responsible for an annual mortality of several species of ungulates. This was confirmed by the German Agency for Technical Cooperation at their Veterinary Diagnostic Laboratory in Dar-es-Salaam where *B. anthracis* was cultured and identified as the cause of death in several species. The most frequently and severely affected species was the area's Ny-

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asa wildebeest (*Connochaetes taurinus johnstoni*).

For 27 mo before, during and after two anthrax epizootics I used the demography of the wildebeest, the patterns of events, an examination of the habitat and a review of the literature for an epidemiological consideration of anthrax, the basis for my thesis (Gainer, 1979, M.S. Thesis, Univ. British Columbia, Vancouver, British Columbia, 203 pp.) from which details of this study can be obtained. The area is adjacent to the Lug'onya River 80 km upstream from the Rufigii River. During the latter part of the wet season, November to May, it becomes a large floodplain and during the dry season, June to October it ceases to flow. The River's presence is the reason for a diversity of habitat types in an otherwise "miombo" tall grass woodland.

Associated with the floodplain was an abundance of plains antelope. During the wet time of the year, wildebeest and several other species concentrated in shortgrass regions and during the dry time of the year most of the animals dispersed into the woodlands.

The short grasslands were divided in two categories, the smaller northern region in which anthrax outbreaks occurred and the larger southern one without such outbreaks. The anthrax area was adjacent to another minor floodplain of a tributary of the Lug'onya River and by standards of range management it was overgrazed and a poor quality environment for grazing animals. Waterholes here were surface collections of warm, murky, alkaline water around which the area's animals concentrated, including several species of vultures.

The larger shortgrass region to the south without anthrax had good range conditions, an abundance of underground water with a neutral pH supplying relatively deep, cool, clear waterholes. Despite the fact that there was considerable movement of herds between the ranges, the disease did not occur in the southern one.

Anthrax mortality coincided with the movement of wildebeest onto the shortgrasses, just prior to the calving season early in December until after their breeding season late in April. Tsetse flies (*Glossina* spp.) were numerous in the wooded areas during the November to May wet season.

Specifically investigating the causes of mortality in this region, I found several hundred carcasses in the vicinity of the overgrazed region and only seven live animals that were weak and unable to keep up with their companions (of four species in all areas). Their collection and necropsy revealed causes of disease other than anthrax. Blood smears collected from nine fresh carcasses were stained with Giemsa or Wright's stain. Individual rod-shaped bacilli with prominent capsules in all nine carcasses was substantial evidence of anthrax. Further proof was two Ascoli precipitin tests on old carcass material and recovery of *B. anthracis* from fresh material from four carcasses. With this I concluded that peracute anthrax was by far the most frequent cause of debilitating disease in this area.

Regular vehicle transects of the wildebeest population throughout the period of the study revealed an exceptionally high proportion of calves and yearling recruitment that often characterizes anthrax epizootics (Brunsdon, 1968, op. cit.). The life table for the population older than calves, constructed from necropsies and skull collections, revealed an exceptionally high mortality rate and short life expectancy compared to other wildebeest populations (Attwell, 1982, Afr. J. Ecol. 21: 147–168). In this study scavenging of carcasses of older animals by predators that otherwise would have killed a great many calves during their most vulnerable first months of life further contributed to the youthfulness of the population. Anthrax carcasses here like in the Serengeti (Mollel, 1977, E. Afr. Wildl. J. 15: 331) had lions (*Panthera leo*) feeding on them. Additional evidence of the compensatory, nonadditive effects from the estimated 11% a year anthrax mortality of animals older than calves was Rodgers' (1980, Ph.D. Thesis, Univ. Nairobi, Kenya, 808 pp.) monitoring of a consistent increase in the population before, during and after this study.

This anthrax area closely resembled that described by Ebedes (1972, Vet. Rec. 90: 198) in which he found spores in the soil near the edges of waterholes in denuded and overgrazed ranges. Thirty-five soil samples from the edges of the water sources in the Selous anthrax area, submitted to the Veterinary Diagnostic Laboratory in Dar-es-Salaam where specific efforts were made to recover spores of *B. anthracis* by Dr. P. Hummel of the German Agency for Technical Cooperation, were found to be negative for the organism. This led me to believe that the great number of animals that had died of the peracute infection in a short period of time in a small area did not have recent oral doses of large numbers of spores. Instead I thought that they must have had what was a low and not necessarily recent dose (either orally from spores in scant numbers and locations that escaped my detection or from the inoculation of the vegetative form by tsetse flies) which experimentally would cause only low level or inapparent infections.

Several clostridia and erysipilas infections are closely related to anthrax and also are associated with peracute infections, specific seasons and specific environments (Blood et al., 1983, op. cit.). Their epidemiology is also unclear but the occurrence of these more common livestock problems is usually not associated with the animal's recent exposure to the organisms. Instead it is clearly recognized that these diseases have a subclinical dormant stage that reverts to the peracute infection when the host's resistance is modified.

In actual fact, several studies have indirectly made reference to similar such features for anthrax. Stein (1948, Vet. Med. 43: 463–469) and Provost and Tronette (1957, Rev. Elev. Med. Vet. Pays Trop. 1: 25–26) cultured *B. anthracis* from the retropharyngeal lymph nodes of otherwise healthy animals indigenous to anthrax areas. Provost et al. (1974, Rev. Elev. Med. Vet. Pays Trop. 17: 39–52) found serological responses to anthrax in indigenous animals as have vaccination programs using the Pasteur types of vaccine (Siegmund, 1967, Merck Veterinary Manual, Merck, Rahway, New Jersey, 1686 pp.).

Such a relationship would explain why overgrazing and other environmental stresses are associated with anthrax areas, why agriculture practices make a difference to the presence of the disease, why bloodsucking insects experimentally thought to be incapable of causing peracute infections are yet commonly associated with the disease (Sens and Minett, 1944, Indian J. Vet. Res. Anim. Husb. 14: 149–158) and may actually be an important means of transmission, and why young-of-the-year would be less affected than older animals.

In summary, two complete epizootics of anthrax were studied in a wilderness area with a history of regular, seasonal outbreaks. Based on the demography of the wildebeest, an examination of the habitat, the pattern of events and a review of the literature, I found many inconsistencies with our concepts of anthrax epidemiology. Instead I found the epidemiology to be more in keeping with our understanding of blackleg and erysipilas infections. That is, the occurrence of the peracute disease in the field was not associated as much with a recent oral exposure to large numbers of spores as it was to the existence of the animal in a habitat over a period of 1 yr or more in which there were low numbers of spores or, via bloodsucking insects the vegetative form. Experimentally such infections have produced relatively mild levels of disease but given the environmental stresses of anthrax areas, they appear to be able to cause the peracute levels of anthrax.

Ian McTaggart Cowan and many other people and organizations contributed to this study and the Miombo Research Center.

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—Danny B. Pence, Editor