

Conserving rhinoceros in the face of disease

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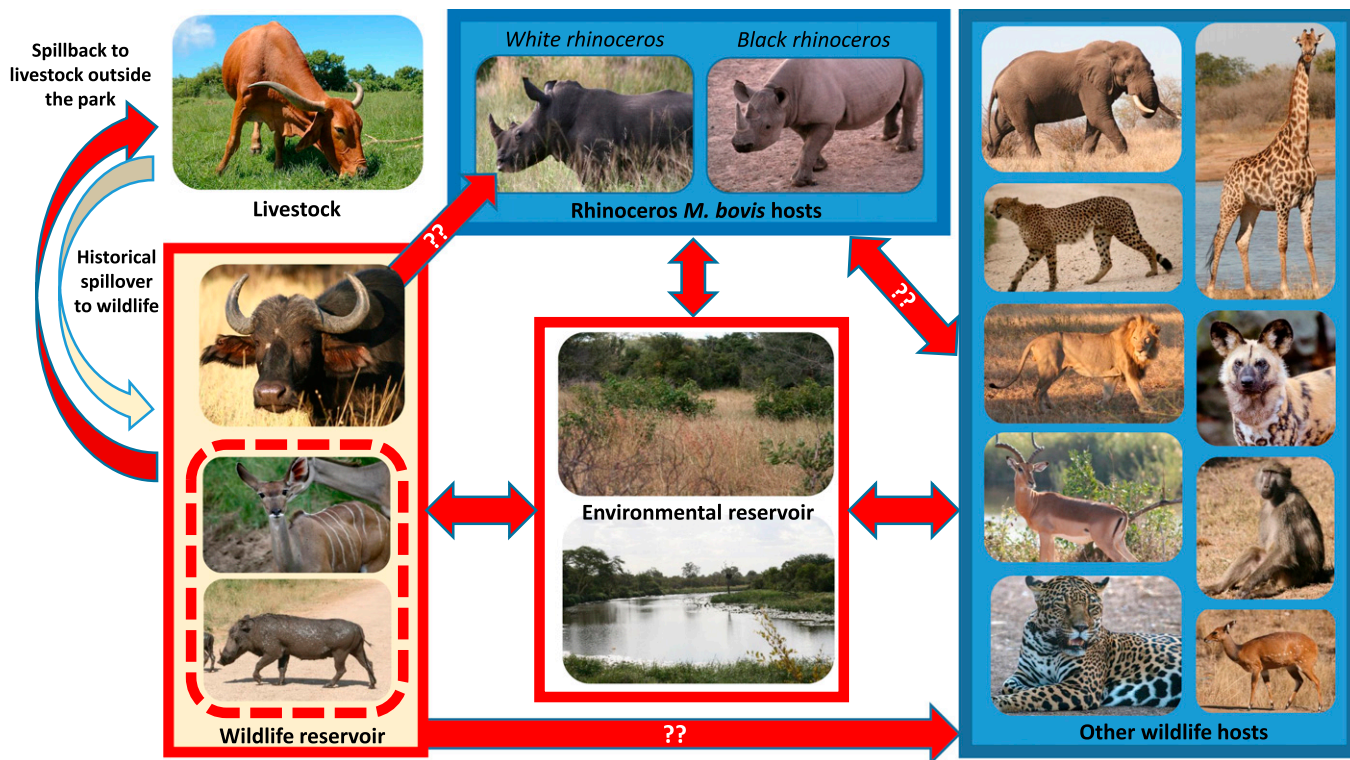


Fig. 1. Potential *M. bovis* transmission routes among livestock, wildlife, and the environment in South Africa. bTB was historically introduced to wildlife by contact with livestock but today is maintained in African buffalo (*S. caffer*) ranging in conservation areas, which are a source of infection to cooccurring wildlife and neighboring livestock. In PNAS, Dwyer et al. (5) examine the epidemiology of *M. bovis* in black (*D. bicornis*) and white rhinoceros (*C. simum*) in KNP, South Africa. They found evidence to suggest buffalo may be a source of infection to rhinoceros. Disease reservoirs, both in wildlife and the environment, are outlined in red. Wildlife reservoir hosts (yellow box) include the key (buffalo) and hypothesized (kudu, *T. strepsiceros* and warthog, *P. africanus*; dashed red line) maintenance hosts. Wildlife hosts with confirmed *M. bovis* infections in KNP are shown in blue boxes, following Bernitz et al. (9). Not all known hosts are shown. Red arrows indicate the hypothesized direction of *M. bovis* transmission, with interspecific transmission believed to occur primarily through a shared environment. Livestock, wild dog, and leopard photos are from the public domain (CC0 Public Domain license). All other photos by P.L.K.

Majestic rhinoceroses once roamed widely across Africa, Asia, and Europe but today are considered threatened or endangered, primarily due to declines driven by the illegal trade of their horns. While conservation efforts have partially succeeded in increasing rhinoceros numbers on the landscape, some populations continue to be at risk due to poaching, habitat loss, climate change, and infectious diseases. In South Africa there are two rhinoceros species, the black (*Diceros bicornis*) and white rhinoceros (*Ceratotherium simum*); in addition to facing pressure from a resurgence in poaching activity (1), bovine tuberculosis (bTB), an infectious disease caused by the bacterial pathogen *Mycobacterium bovis*, was recently reported in both species within conservation areas (2, 3). The extent and health effects of *M. bovis* infections in wild rhinoceroses remain unknown and bTB has been deemed an “underrecognized threat” to their conservation (4). In PNAS, Dwyer et al. (5) examine the prevalence, distribution, and risk factors of *M. bovis* infections in rhinoceros of Kruger National Park (KNP), South Africa, home to the largest population of free-ranging rhinoceroses in the world.

bTB is a chronic, progressive disease that primarily affects livestock and is a significant public health concern. Disease outbreaks can result in devastating economic losses that jeopardize the livelihoods of livestock and dairy producers, particularly in developing countries (6). The pathogenic agent, *M. bovis*, belongs to a group of bacteria causing tuberculosis in mammals known as the *Mycobacterium tuberculosis* complex (7). As a generalist pathogen, *M. bovis* can infect a broad range of domestic and wild host species

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(8, 9); *M. bovis* infections have been detected in at least 24 South African wildlife species to date (9), with genetic data suggesting pervasive transmission within and between species (8). In addition to black and white rhinoceros, *M. bovis* infections have been documented in several other species of conservation concern, including cheetahs (*Acinonyx jubatus*) and wild dogs (*Lycaon pictus*) (10, 11).

Dwyer et al. (5) demonstrate *M. bovis* infections are widespread in both black and white rhinoceros in KNP. This finding has important implications for the conservation and management of rhinoceros as well as other vulnerable species within bTB-endemic areas. Control policies for bTB often are centered on quarantine and movement restrictions (12), which may impede conservation efforts that rely on translocating animals to establish or enhance existing populations outside conservation areas. The relatively high *M. bovis* prevalence observed in a key rhinoceros source population highlights the need for systematic testing to detect active infections and extended quarantine to mitigate the spread of bTB among rhinoceros populations, as well as other domestic and wild hosts.

bTB is endemic in KNP (13), where African buffalo (*Syncerus caffer*) are a key maintenance host for *M. bovis* and may be a continual source of infection to neighboring game and livestock herds as well as cooccurring wildlife (14). Dwyer

feeding on grasses close to the ground. Transmission among rhinoceroses may enable further spread of the pathogen. Alternatively, other potential wildlife reservoirs, such as the greater kudu (*Tragelaphus strepsiceros*) and warthogs (*Phacochoerus africanus*) (13), may also play a role in bTB spillover to rhinoceros as well as other species.

Identifying spatiotemporal patterns in pathogen infections can inform predictions of transmission risk within and between host species. Dwyer et al. (5) show that *M. bovis* infections in rhinoceros varied over time and space, shedding light on when and where transmission risk may be highest for wildlife and neighboring livestock herds. Notably, the authors found *M. bovis* infection in KNP rhinoceros varied by ranger area and ecozone (5). While mean bTB prevalence in rhinoceros was ~15%, prevalence reached as high as 30 to 40% in the southwest corner of the park (Pretoriuskop), a region where a significant cluster of infected white rhinoceroses was also detected. Furthermore, this area shares much of its border with farmland in the Mpumalanga Province, and high disease risk along this border is a considerable threat to surrounding communities that depend on livestock farming. While fencing is in place to prevent contact between livestock and wildlife, it is not impermeable to the movement of some species and may also be compromised by flooding or elephants.

M. bovis infection risk decreased in black rhinoceros over time, suggesting temporal changes in environmental factors or host population dynamics may affect transmission in this species. Previous work in KNP revealed that drought conditions may increase mixing of buffaloes among social groups and promote *M. bovis* transmission (18). Therefore, it

is plausible transmission to black rhinoceros may be driven by temporally fluctuating environmental factors that alter the species' distribution and contact rates with infected hosts or contaminated areas. For example, drier conditions may promote larger aggregations of mixed-species groups at limited water sources, increasing both intra- and interspecies pathogen transmission. Further investigation into environmental or host drivers of *M. bovis* transmission are needed to better understand differences in infection dynamics observed across species.

Whether *M. bovis* infections may compromise rhinoceros health and affect population dynamics remains an open question requiring further investigation. Disease susceptibility and pathology appear to differ among species, with varying degrees of clinical symptoms (7). Previous cases in zoological settings have shown that rhinoceroses are susceptible to tuberculosis disease (19), though experimental infection of white rhinoceros indicates young, healthy animals may be able to resist the pathogen and limit disease progression (20). Dwyer et al. (5) found no association between infection and clinical symptoms and most (83%) cases in rhinoceroses were normal. Nonetheless, latent infection has been speculated, such that disease symptoms may develop later in life (20), a phenomenon that has been well-documented for human tuberculosis. Further longitudinal studies that follow disease progression in infected wild rhinoceroses would provide insight into

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et al. (5) found that *M. bovis* infection risk increased with the number of buffalo herds within an individual's home range, confirming a significant role for buffalo in *M. bovis* transmission to rhinoceroses. Interestingly, the authors did not similarly find an association between overlapping buffalo herds and black rhinoceros infection risk. Taken together, species-specific variation in risk factors provides important clues about potential transmission routes within a disease system. For example, from these results we could posit *M. bovis* transmission to white rhinoceros occurs through spillover from the buffalo reservoir, whereas transmission to black rhinoceros may be through alternative means (Fig. 1).

M. bovis can spread through direct contact of respiratory secretions between individuals, but it is hypothesized that indirect interaction through a shared resource is the most probable mode of transmission among species (15). Pathogen shedding in feces has been documented in buffalo (16) and, thus, spillover to rhinoceros may occur through a contaminated environment, such as a waterhole or foraging site (Fig. 1). White rhinoceroses are grazers with habitat and foraging preferences similar to those of buffalo (17), whereas black rhinoceros are browsers; species differences in foraging and vegetation preferences may not only influence the degree of habitat overlap with buffaloes (and thus opportunities for direct transmission) but may also affect the probability of indirect pathogen exposure through ingestion, with higher exposure for white rhinoceros

whether bTB may affect survival or reproduction in a natural system.

Dwyer et al. (5) present findings on the epidemiology of a zoonotic pathogen in a complex multiple-host wildlife disease system. Given the consequences of bTB to both human and animal health, this study emphasizes the urgent need for ongoing *M. bovis* surveillance in bTB-endemic areas and the adoption of management strategies that consider multiple hosts and transmission pathways. Further work is also

needed to better understand the variation in bTB susceptibility and pathogenesis among species, as well as effects of tuberculosis disease on population-level fitness. This study provides vital insights for understanding and managing emerging pathogens in multihost disease systems and also highlights the importance of mitigating impacts of infectious diseases to vulnerable species, such as the iconic black and white rhinoceros, to ensure their long-term viability.

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