

Human behavior influences infectious disease emergence at the human–animal interface

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Although human behavior is frequently cited as a factor influencing the emergence of disease at the human–animal interface, few empirical studies have demonstrated this relationship. We compare humans and their domestic animals living in close proximity to populations of the endangered African wild dog (AWD, *Lycaon pictus*) in both Kenya and Botswana. We identify culturally based differences in domestic-stock grazing practices among pastoralists that strongly influence frequency of contact between domestic dogs and AWDs, with parallel differences in disease-related mortality in AWD populations. Using this study and other examples, we illustrate a conceptual model of the interaction between human behavior and emerging infectious diseases at the human–domestic-animal–wildlife interface. Human cultural behavior has the potential to influence pathogen adaptation, host susceptibility, spatial distribution, and pathogen exposure and contact rates between susceptible hosts, reservoir hosts, and pathogen communities. This affects the pathogen's basic reproductive number (R_0), ability to invade, and persistence potential. Human behavior may be the key that unlocks the proverbial Pandora's Box, allowing infectious diseases to emerge.

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Human behavior, partially or wholly determined by cultural practices, exerts a powerful influence on pathogen invasion dynamics and the spread of infectious disease within human populations, as seen in the emergence of sexually transmitted diseases such as human immunodeficiency virus (HIV; Morse 1995). Although human behavior is identified as a factor that influences disease emergence events (Parrish *et al.* 2008), few studies have focused on the interactions between human behavior and pathogen emergence. Rather, behavioral research thus far has largely concentrated on the pathogen, reservoir hosts, and/or the vectors of infectious diseases. Yet behavior and cultural practices strongly shape differences in what humans do and how they interact with the environment. This includes culturally shaped relationships with domesticated animals and, by extension, the interactions that humans and domestic animals have with sympatric wildlife, the environment, and pathogen communities.

We begin with an examination of the influence of human behavioral differences on pathogen transmission between domestic dogs and an endangered species, the African wild dog (AWD, *Lycaon pictus*; Figure 1), in Botswana and Kenya. Common canine diseases have been implicated in the decline of the AWD, with domestic dogs identified as the primary source of these infections (Woodroffe *et al.* 1997). Here, we examine how host con-

tact rates and pathogen transmission might be influenced by the divergent cultural practices of pastoralists in these two countries. Using this investigation and other examples, we illustrate a conceptual model of the influence of human behavior on disease emergence and discuss its implications for infectious disease research and control.

Methods

We used data from a comparative study conducted in Kenya and Botswana from 1989–93. This dataset presented an opportunity to investigate, retrospectively, the relationship between divergent cultural practices of pastoralists and contact between domestic dogs and AWDs.

Study area – Kenya and Botswana

The Kenyan study site was located in the Masai Mara National Reserve and surrounding Maasai tribal lands. During that time, AWD density ranged from 0.020–0.034 animals km^{-2} , and average pack home range measured 660 km^2 (Fuller *et al.* 1992).

The Botswana study site was located in the Okavango Delta ecosystem. AWD population perimeters and density (0.017 animals km^{-2}) were comparable to those of Kenya, with an average pack home range of 617 km^2 (McNutt 1996).

Mortality and contact

We surveyed households using a questionnaire format to collect data on domestic dog mortality and contact with

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AWDs in both study sites during the study period. Respondents were asked to identify the household-dog population and number of dogs that died over the past year, according to type of mortality (sickness, killed by humans, injured/died or killed by wildlife, other causes of mortality, and disappeared/unknown). We also asked the respondents whether their household's dogs remained at home or accompanied grazing cattle and whether domestic dogs had any direct contact with other wild carnivore species.

Kenya

As a result of distance limitations, study *manyattas* (human settlements composed of several huts grouped together, where family groups live) were randomly selected within the core area of the Aitong Pack, the largest of the study AWD packs in the region. The number of *manyattas* sampled varied between years as family groups split or merged. An elder Maasai tribesperson was selected each year from each study *manyatta* to answer a prepared questionnaire. The same Maasai interpreter, fluent in both English and the tribal language (Maa), was used each year, to ensure accurate communication.

Botswana

Two villages, Sankoyo (19° 30'S, 23° 15'E) and Khwai (19° 10'S, 23° 45'E), both located within the home range of the study animals, were selected. Within each village, heads of households who owned domestic dogs were randomly selected and interviewed by the same Botswana Youth Service volunteer, who was fluent in both English and Setswana.

Disease-specific mortality and contact between domestic dogs and AWDs were calculated from responses to questionnaires (domestic dogs) or observational data (AWDs, five and eight study packs in Kenya and Botswana, respectively). We defined disease mortality for both AWDs and domestic dogs in the same manner as the number of dogs that died of disease, divided by the total number of dogs that died during the observation period. Domestic dogs that disappeared from a household were presumed dead of unknown causes. AWDs between 2 and 3 years old disperse from their natal packs in same-sex groups (McNutt 1996); when groups of individuals in that age range disappeared from packs, they were assumed to have dispersed. AWDs that disappeared, but were unlikely to have dispersed (eg age or number of dogs disappearing such as single animals), were considered to have died of unknown causes. Domestic dogs or AWDs that were observed with disease symptoms before disappearance were assumed to have died of disease. Mortality analyses



Figure 1. The African wild dog (*Lycaon pictus*) is one of the most endangered canid species in the world. Human behavior may be contributing to the decline of this species.

were restricted to adult age classes (domestic dogs as defined by the eruption of canine teeth; AWDs > 1 year of age). Individual AWDs are identifiable by unique coat markings and most study animals were known since birth or age was estimated through individual and pack history. Data categories by year and location were analyzed with Yates-corrected chi-square tests.

Results

We found significant differences in the ranging behavior of domestic dogs (Figure 2). The majority of Kenyan respondents (88%) indicated that their domestic dogs spent the day with the grazing cattle, accompanied by herders, whereas most Botswana respondents (93%) asserted that domestic dogs typically remained at home or in the village, since cattle were normally left to graze free-range unattended (1992, $\chi^2 = 40.551$, $P < 0.0001$; $n = 41$ and 28 household surveys, respectively). Subsequent studies by the authors on herding practices and domestic dog use in Botswana substantiate these findings (KAA unpublished data), as did observations made by the authors in both sites during this study.

There was no significant difference in the proportion of disease-specific mortality in domestic dogs sampled among homes/*manyattas* in Botswana and Kenya in 1992 (Botswana: 81%, $n = 27$ deaths; Kenya: 86%, $n = 155$ deaths; $\chi^2 = 46$, $P > 0.05$). However, AWD mortality associated with disease in Kenya was high in all 3 years (95%, 1989–1991, $n = 41$ deaths). No disease-related mortality was identified in Botswana AWDs from 1991–1992 ($n = 35$ deaths). Indeed, no disease-related mor-

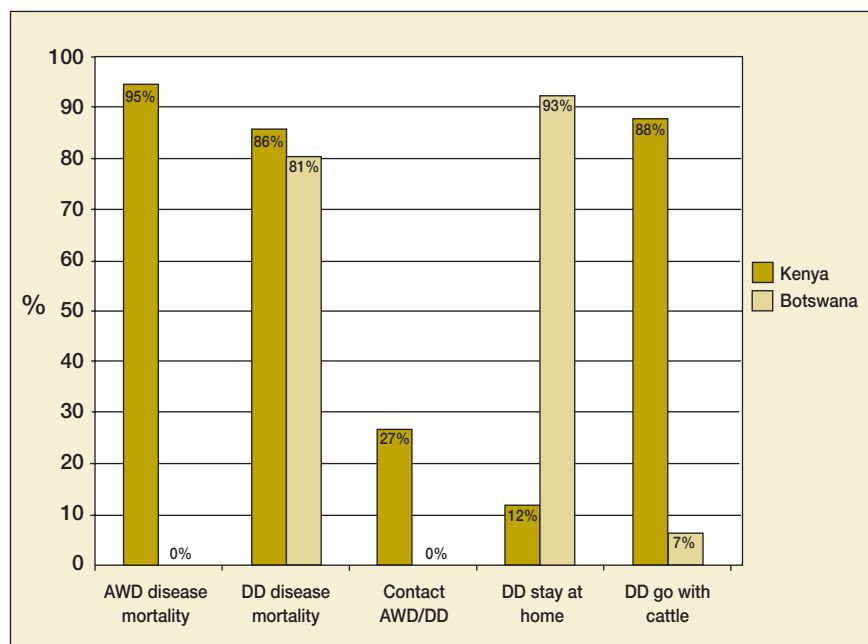


Figure 2. The proportion of disease-specific mortality and contact between African wild dogs (AWD) and domestic dogs (DD) compared to domestic dog ranging behavior in the Kenya and Botswana study sites.

tality was identified in this AWD population until 1995, despite intensive surveillance (Alexander *et al.* 2008). Contact between AWDs and domestic dogs was identified only in the Kenyan study site (1990, 27%, $n = 30$ household questionnaires). Of households reporting contact, 37% indicated that there had been direct physical conflict between the two canid species resulting in DD mortality. After the last known AWDs died in the Kenyan study area in early 1991, respondent reports of contact between domestic dogs and AWDs decreased significantly (2%, 1991–1993, $\chi^2 = 16.3$, $P < 0.0001$, $n = 128$ household questionnaires). Botswana respondents reported no contact between their domestic dogs and AWDs (1992, $n = 28$ household questionnaires).

Discussion

In this study, host contact rates and pathogen transmission potential were influenced by the divergent cultural practices of pastoralists. A conceptual model of the role of human behavior on pathogen emergence at the human–domestic–animal–wildlife interface (Figure 3) identifies four key areas where this influence can occur: (1) host adaptation, (2) host range and spatial overlap, (3) host population ecology and contact, and (4) host physiology and pathogen invasion potential. We discuss each of these separately below and provide additional examples that illustrate the impact of human behavior on disease emergence at this interface.

Host adaptation

In Asia, cultural practices in food retailing (eg live animal markets, known as “wet markets”) have been identi-

fied as providing a distinctive epicenter for pathogen adaptation. This can operate through various mechanisms, including genetic reassortment, recombination, and mutation arising from close contact between pathogens, live animal species (domestic and wild), and humans (Woo *et al.* 2006). The popularity of Asian wet markets continues to prevail over that of modern supermarkets, even in developed Asian economies, as a result of cultural preferences for fresh meat (the chilling or freezing of which is perceived as detrimental to quality) from slaughtered animals purchased live (Goldman *et al.* 1999). Wet markets constitute pathogen adaptation opportunities and have been linked to newly evolved and emerging pathogens, such as severe acute respiratory syndrome (SARS; Brown 2004; Woo *et al.* 2006). Such locations will provide important opportunities for directed surveillance

and detection of emerging pathogens recently adapted to previously unrecognized human, wildlife, and/or domestic animal hosts.

Jones *et al.* (2008) identify the majority of emerging infectious disease pathogens as either bacterial or rickettsial in origin (54.3%); a large proportion of these are directly related to the emergence of drug-resistant bacterial strains, each identified as separate emerging infectious disease events. Human behavior has influenced pathogen evolution through the inappropriate use of antibiotics in both humans and animals. Gilchrist *et al.* (2007) estimate that – annually in the US – over 11 million kilograms of antibiotics are used in livestock, primarily to promote growth, and 1.4 million kilograms are used for medical purposes in humans. Concerns over the increasing incidence of antibiotic resistance have led to pressure for the US Government to limit antibiotic use (Gilchrist *et al.* 2007).

Host range and spatial overlap

Human societies have adapted culturally to widely variable and specific environments across the globe. Culturally embedded human activities have the potential to shape the distribution of host species (reservoir and susceptible), pathogen communities, and their associated vectors. One example of this can be seen in Chagas disease (*Trypanosoma cruzi*) in humans in the Amazon region of South America. Highland Amerindians – endemically infected with Chagas disease – lived in higher densities than lowland populations, were comparatively sedentary, and reared domestic animals (in particular, Brazilian guinea pigs [*Cavia aperea*], an important vector host and pathogen reservoir) in and near their

homes. These behaviors are thought to result in favorable conditions for the domiciliation (successful home invasion) of blood-sucking triatomine bugs (*Triatominae*) known to transmit the Chagas pathogen to humans. In contrast, lowland Amerindian populations lived in small settlements, were highly mobile, and did not raise domesticated guinea pigs. As a result, there was no domiciliation of the vector and transmission of the pathogen in lowland populations (Coimbra 1988).

Human behavior can also influence the spatial distribution of a pathogen, allowing exposure to new susceptible hosts; one example of this is the supplementary provisioning of food to wild animals. This human behavior has been associated with the outbreaks of *Salmonella* spp in various wild passerine bird species fed salmonellae-contaminated feed (Dobson and Foutopoulos 2001).

Similarly, the culturally shaped human behavior of keeping household pets, such as domestic cats, has probably contributed to the increased spatial distribution of the zoonotic protozoan parasite *Toxoplasma gondii*, for which felids are the definitive host. Stormwater contamination of coastal marine ecosystems with *T. gondii* is largely attributed to pet fecal waste in the environment, and has resulted in the successful emergence of *T. gondii* in a novel host, the southern sea otter (*Enhydra lutris nereis*) (Dobson and Foutopoulos 2001; Dabritz *et al.* 2006).

Host population ecology and contact

For directly transmitted pathogens, contact is a necessary prerequisite for pathogen spillover (transmission between reservoir and susceptible host species). We present data that identify culturally based differences in domestic-stock grazing practices of pastoralists; these strongly influence contact and potential pathogen exposure between domestic dogs and AWDs. In both study sites, pastoral livestock-production systems were used by rural communities. In Kenya, however, Maasai tribal people had a culture of livestock husbandry with intensive management of livestock by herders typically accompanied by domestic dogs (Maundu *et al.* 2001). In contrast, livestock farmers in Botswana (representing various tribal groups) rarely herd or attend grazing cattle and practice a much more passive approach to livestock care (Hemson 2003).

In Kenya, where dogs remained with cattle and herders, contact with AWDs occurred frequently and disease-related mortality among the sympatric AWD population was high. This population of AWDs was extirpated from the region in 1991, and canine diseases were causally implicated (Alexander and Appel 1994; Kat *et al.* 1995). In contrast, in Botswana, farmers and their domestic dogs

rarely accompany their free-ranging cattle, and neither contact between domestic dogs and AWDs nor disease-related mortality in AWDs were recorded. Several factors could contribute to the observed differences in AWD mortality at the two study sites, including a suspected outbreak of canine distemper virus (CDV) in the Kenya study site in 1991 (Alexander and Appel 1994). However, AWD disease mortality was high in Kenya before this CDV outbreak, when the last of the wild dogs disappeared from the study area. Human behavior and cultural practices changed the frequency of direct contact between susceptible AWDs and the primary reservoir for canine infectious diseases (ie domestic dogs), thereby changing pathogen transmission potential in susceptible AWDs.

Another important example of the influence of human culture on contact between hosts and pathogen spillover is the hunting and consumption of non-human primates, identified as a high-risk activity that allows cross-species transmission of pathogens to occur between humans and non-human primates (Bowen-Jones and Pendry 1999). Consumption of primate species by humans is not universal in sub-Saharan Africa, but is based on cultural practice. Although there is a recognized culture of primate utilization in west and central Africa (Bowen-Jones and Pendry 1999), people in southern African countries, such as Botswana, do not hunt or eat non-human primates, although they do consume other types of bushmeat (Botswana Department of Wildlife and National Parks; Antipoaching Unit Data 1994–2006). Contact between people and non-human primate tissue or fluids is extremely uncommon and is actively avoided. Thus, while non-human primate pathogens may occur in non-human primate populations, which overlap spatially with human populations, regional differences in human behavior are an important predictor of the risk of direct contact and pathogen transmission potential. This information is fundamental to the design of disease surveillance programs for the early detection of potential human pathogens of non-human primate origins.

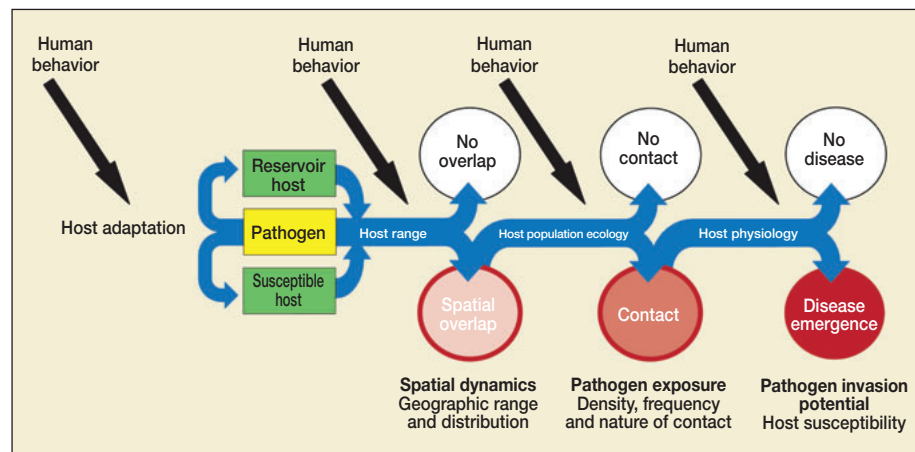


Figure 3. A conceptual model of the potential influence of human behavior on pathogen emergence at the human–domestic-animal–wildlife interface.

Host physiology and pathogen invasion potential

Human behavior and cultural practices can also have important consequences for host physiology and can influence pathogen invasion potential through changes in host susceptibility and resistance. Through a series of viral challenge studies where human subjects were exposed to viruses associated with the common cold, Cohen (2005) and others have demonstrated that there is a positive relationship between physiological stress, social network composition, early childhood socioeconomic status, and increased susceptibility to respiratory illness. Rather than direct suppression of the immune system, chronic stress may influence host resistance by altering the immune system's response to hormonal signals and the regulation of pro-inflammatory cytokines (Cohen 2005).

Urbanization is identified as an important factor influencing infectious disease processes in wildlife populations (Bradley and Altizer 2007). Wildlife malnutrition in urban landscapes can lead to immunosuppression, increased levels of parasitism, and mortality. The supplementary feeding of wildlife can expose hosts to new pathogens or influence contact rates with infected hosts, but may also improve host condition and increase immune function and pathogen resistance of individuals within food-supplemented populations (Bradley and Altizer 2007). Thus, we see the bidirectional possibilities associated with human behavior and disease emergence.

Conclusions

Human cultural behavior has the potential to influence pathogen adaptation, spatial distribution, exposure, and contact rates between susceptible populations, reservoir hosts, and pathogen communities. Such behaviors can also influence host susceptibility, affecting the basic reproductive number (R_0) of the pathogen (Dobson and Foufopoulos 2001) and the pathogens invasion and persistence potential. These examples illustrate the importance of human cultural differences and behavior in determining the spatial patterns of pathogen exposure and invasion risk for emerging infectious diseases. Understanding the relevant characteristics of human cultural behavior could prove essential in the development of targeted surveillance of emerging infectious disease at the human–animal interface, as well as in the application of appropriate local public health strategies designed to prevent future pandemics. To do this effectively, greater inclusion of the social sciences will be essential, as researchers strive to attain predictive capability in emerging infectious disease research.

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