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Domestic mammals facilitate tick-borne pathogen transmission networks in South African wildlife



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ABSTRACT

As changes in the environment have brought wild and domestic animals into closer proximity, cross-species disease transmission has become a major concern in wildlife conservation. The worldwide impacts of tick-borne diseases require an understanding of pathogen transmission dynamics across different host species. Livestock are often kept near protected areas and frequently share habitat with wild animals. The influence of host community composition on tick-borne pathogen transmission remains poorly understood, making it difficult to determine whether sharing habitats with domestic livestock increases tick-borne disease in wildlife populations. We used network analysis to analyse 35,349 collections of 54 tick species in South Africa, treating hosts as nodes and shared tick species as links. Across all life stages, 93 mammalian species were connected by a total of 3105 links. Sheep, goats, and dogs were particularly important domestic species for network connectivity; and for wild animals, soft-skinned, smaller mammals such as the scrub hare. Although South African ticks exhibit some specialization on wild animals, network analysis showed that opportunistic feeding on domestic hosts can lead to shortened transmission pathways and facilitate pathogen spread between mammal species. Mammal species are highly interconnected through the tick species that they share, and domestic mammals significantly increase the risk of disease transmission. These findings support conservation measures that limit contact between domestic and wild mammals to reduce tick-borne disease transmission. Grazing in protected areas must be evaluated in light of disease risks to both domestic and wild animals, and potentially also to people.

1. Introduction

Infectious diseases are an important and growing concern for conservation, with changes in disease prevalence, diversity, and severity occurring rapidly as the earth's environment is changed by people. Cross-species disease transmission and the (re)emergence of pathogens from wild reservoirs are often facilitated by anthropogenic activities (Antia et al. 2003; Lubroth 2012). Climate change, for example, can alter the geographic distribution of arthropod vectors, augmenting the risk of infectious disease transmission in wild species and the incidence of zoonoses in humans (Cumming and Van Vuuren 2006; Garamszegi 2011). Human activities and associated landscape changes are bringing domestic animals, wild animals and humans into increasingly closer proximity in many places, resulting in reciprocal exchanges of pathogens (Pastoret et al. 1988; Daszak et al. 2001; Patz et al. 2004; Prager et al. 2012a; Hegglin et al. 2015; Han et al. 2016; Hassell et al. 2017). In southern Africa, the wildlife trade and wildlife translocations into conservation and hunting areas near livestock ranches and rural subsistence communities further increase such contacts, in addition to causing stress and undermining the immune systems of wild animals (Karesh et al. 2005; Penzhorn 2006; Chomel et al. 2007). As a result, the increasing anthropogenic alteration of natural environments offers numerous opportunities for generalist pathogens and cross-species pathogen transmission, with negative implications for wildlife, protected areas, and human health (Dobson and Foufopoulos 2001; Altizer et al. 2003; De Vos et al. 2016).

Although wild animals were historically considered natural reservoirs of many infectious diseases of domestic animals (Taylor and Martin 1987), transmission from domesticated species to sympatric wildlife has become a major problem for conservation (Daszak et al. 2000; Daszak et al. 2001; Prager et al. 2012a). Over a quarter of domestic mammal pathogens are infectious to wildlife species (Cleaveland et al. 2001). For example, canine distemper outbreaks recorded in lion populations in the Serengeti National Park were initiated by domestic

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dogs, but also affected silver-backed jackals, bat-eared foxes, and African wild dogs (Roelke-Parker et al. 1996; Prager et al. 2012b). Livestock parasites that are shared with African wildlife include rinderpest between cattle and African buffalo, eland and greater kudu; brucellosis between cattle and African buffalo and hippopotamus; foot and mouth disease between cattle and African buffalo; African swine fever between domesticated swine and the common warthog; and bovine tuberculosis between cattle and African buffalo, greater kudu, common duiker and lechwe (Pastoret et al. 1988).

The complexity of the problem of understanding the relative influences of wild and domestic hosts on parasite and pathogen dynamics is increased by host generalism. Many parasites and pathogens can infect multiple host species (Woolhouse et al. 2001; Keesing et al. 2006). The generalist capacity of such pathogens has been linked to pathogen genetic variability and abundant opportunities for cross-species transmission (Woolhouse et al. 2001). However, multi-host pathogen dynamics in host communities remain poorly understood. Previous studies have shown that host species diversity can affect the prevalence of some pathogens, whilst infectious diseases can in turn influence host community structure (Power and Mitchell 2004; Keesing et al. 2006). Multihost-multi-parasite systems are complex, but it is clear that within these systems, all species are not equal. Some hosts may be particularly susceptible to infection, and some vectors may be particularly good at transmitting particular pathogens. Epidemic disease outbreaks, for example, often arise via a reservoir species which maintains a relatively high pathogen population and from which pathogens spill over to other hosts (Daszak et al. 2000; Power and Mitchell 2004).

Tick-borne diseases are a major concern all over the world, including North America and Europe, with high impacts on public health and animal health (Jongejan and Uilenberg 2004). Therefore, understanding differences in pathogen transmission cycles via ticks of wild and domestic hosts is of global conservation importance. In this paper, we explore the roles of wild and domestic mammalian hosts in transmission networks for tick-borne pathogens in South Africa. In particular, we were interested in how alternative conservation approaches, and particularly those that mix wildlife and domestic stock (such as those that allow the coexistence of domestic and wild animals in the same grazing or rearing area, and the presence of domestic animals nearby or inside protected wild areas; Pastoret et al. 1988) versus those that keep them separate (such as using artificial barriers around protected areas; Hayward and Somers 2012), may affect the potential for exchanges of ticks and tick-borne pathogens. In many East African protected areas (e.g., the Serengeti, Masai Mara), cattle are permitted to graze on the edges of protected areas. By contrast, in southern Africa, protected areas (e.g., Kruger National Park, Hluhluwe-Imfolosi National Park) often have electrified fences that prevent contact between larger wild and domestic mammals. These distinctions have been well documented in the context of lion conservation: Packer et al. (2013), for example, have shown that in fenced reserves, lions are primarily limited by density dependence, while in unfenced reserves their population dynamics correlate strongly with human population densities in surrounding communities and density-independent factors dominate.

The feeding behaviour of ticks on different host species creates a system of multiple interconnections that can be viewed as a network, in which hosts are linked by the ticks they share (i.e., intensity of infestation; Caron et al. 2012). Previous studies that have used network analysis to examine the dynamics of parasite infections between individuals of the same host species (Godfrey et al. 2009; Godfrey et al. 2010; MacIntosh et al. 2012) have shown that higher levels of network connectivity tend to increase individual risk of infection and that some parasites may enhance transmission opportunities through their influence on host behaviour (Godfrey et al. 2009). Networks of contacts between different host species and their consequences for pathogen dynamics in multi-species systems have been less investigated, but have the potential to make important contributions to our understanding of multi-host parasite and pathogen transmission pathways (Jeger et al.

2007; Olesen et al. 2008; Salathé and Jones 2010; Pilosof et al. 2015).

We undertook network analysis of an extensive new dataset of 35,349 tick-host interactions to assess the connectivity between 93 South African mammal hosts (85 wild mammals and eight domestic mammals) based on the tick species that they share. For this analysis we focused on the potential niches of ticks and their hosts, rather than their realised niches, in order to achieve a broad national-level overview; we did not attempt to filter host-parasite networks by finer-scale influences on tick occurrences, such as microclimate, topology, and heterogeneity in vegetation structure (Cumming 2002). We used the analysis to identify the most highly connected hosts that facilitate potential tickborne disease transmission, and explore the likely effects of domestic species on these associations. We hypothesised (H1) that since many South African ticks show some degree of specialization on wild animals but feed freely on domestic hosts (Cumming 1998; Cumming 1999; Espinaze et al. 2016), adding domestic species to the network should shorten transmission pathways (i.e., by providing shorter routes between different species) and facilitate the spread of pathogens. Alternatively (H2), if ticks were wildlife specialists or pure generalists, adding domestic hosts should have little impact on the spread of pathogens because doing so would either not add new connections to the network or because the network would be highly interconnected independently of the presence of domestic species.

2. Material and methods

2.1. Data

The dataset used in this study results from 36 years of tick collection by Prof. Ivan Horak in South Africa. Each tick sampled was either collected from a living or a dead host. A total of 35,349 collections (a collection is defined as occuring whenever one or more ticks of a given species were obtained from a single host) of 54 tick species (from eight genera, family Ixodidae) (Appendix A), obtained from 93 mammal host species (85 wild mammals and eight domestic mammals) (Appendix B) were included in the analyses. For each collection, the tick species, life stage (larva, nymph or adult), number of individual ticks collected, mammalian host species, host health condition, geographic location of the sample, and date of collection were recorded. Occasionally the host species was not known, but its genus or family was indicated (e.g. Genetta sp. for genets). Hosts that have been included belonged to 11 orders of mammals: Carnivora (29 spp.), Cetartiodactyla (30 spp.), Rodentia (14 spp), Primates (3 spp.), Perissodactyla (6 spp.), Macroscelidea (4 spp.), Lagomorpha (3 spp.), Proboscidea (1 sp.), Hyracoidea (1 sp.), Eulipotyphla (1 sp.), and Soricomorpha (1 family, Soricidae).

2.2. Network construction

Mammal host species were represented as nodes (vertices) in the network, and tick species shared by pairs of hosts were represented as edges (links). Edges were weighted by the numbers of different tick species shared by each pair of hosts. Since all mammals could work as both donors and recipients of pathogens, the network system was considered "undirected" (Proulx et al. 2005; Poulin 2010). Tick host specificity varies with life-stage (Espinaze et al. 2016), and so three networks were built: a network of hosts sharing all ticks (regardless of life stage), a network of hosts sharing juvenile (i.e., larva and nymph) ticks, and a network of hosts and the tick species they shared were generated using SQL-queries in a relational database.

2.3. Measurement of network structure

Quantification of the network structure was achieved by exploring i) network and ii) node properties, in order to investigate i) system-wide Download English Version:

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