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Impacts of heterogeneous host densities and contact rates on pathogen transmission in the Channel Island fox (*Urocyon littoralis*)

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ABSTRACT

Diseases threaten wildlife populations worldwide and have caused severe declines resulting in host species being listed as threatened or endangered. The risk of a widespread epidemic is especially high when pathogens are introduced to naïve host populations, often leading to high morbidity and mortality. Prevention and control of these epidemics is based on knowledge of what drives pathogen transmission among hosts. Previous disease outbreaks suggest the spread of directly transmitted pathogens is determined by host contact rates and local host density. While theoretical models of disease spread typically assume a constant host density, most wildlife populations occur at a variety of densities across the landscape. We explored how spatial heterogeneity in host density influences pathogen spread by simulating the introduction and spread of rabies and canine distemper in a spatially heterogeneous population of Channel Island foxes (*Urocyon littoralis*), coupling fox density and contact rates with probabilities of viral transmission. For both diseases, the outcome of pathogen introductions varied widely among simulation iterations and depended on the density of hosts at the site of pathogen introduction. Introductions into areas of higher fox densities resulted in more rapid pathogen transmission and greater impact on the host population than if the pathogen was introduced at lower densities. Both pathogens were extirpated in a substantial fraction of iterations. Rabies was over five times more likely to go locally extinct when introduced at low host density sites than at high host-density sites, leaving an average of > 99% of foxes uninfected. Canine distemper went extinct in > 98% of iterations regardless of introduction site, but only after > 90% of foxes had become infected. Our results highlight the difficulty in predicting the course of an epidemic, in part due to complex interactions between pathogen biology and host behavior, exacerbated by the spatial variation of most host populations.

1. Introduction

The ecology of disease in wildlife populations is complicated and often unpredictable, making the management of dangerous health risks an ongoing and adaptive process. One of the primary determinants of infectious disease dynamics is the rate of pathogen transmission from infectious to susceptible hosts (McCallum et al., 2001). For pathogens that are passed directly between hosts, the rate of transmission is strongly affected by the frequency, duration, and type of contact between infected hosts and conspecifics. How frequently potentially disease spreading contacts occur varies with the number of neighboring conspecifics and the amount of contact those neighbors have with one another (Woodroffe, 1999). Neighbor interactions in turn depend on the density of the population, home range sizes, and the amount of overlap between home ranges (McCallum et al., 2001; Sanchez and Hudgens, 2015), all of which vary across space in wild populations.

Host densities and contact rates among neighbors are likely to vary spatially due to differences in the distribution of required habitats and resources. Vegetation and habitat types are often patchy in distribution, leading to areas that contain more favorable habitat types being used more frequently or supporting higher population densities than areas with less favorable habitat types (Lawes and Nanni, 1993; Simcharoen et al., 2008; Turner, 2009). Similarly, resources such as food and mates are rarely distributed uniformly. The size of home ranges and the degree of overlap individuals tolerate with their neighbors can vary with the density of resources within the home range (Dill et al., 1981; Erlinge et al., 1990; Marshall and Cooper, 2004). Interspecific competition for resources also influences density (Vucetich and Creel, 1999; Berger and Gese, 2007) through changes in the number of neighboring home ranges an individual has (Woodroffe et al., 2006; Sanchez and Hudgens,

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