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Modelling landscape effects on density–contact rate relationships of deer in eastern Alberta: Implications for chronic wasting disease

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ABSTRACT

Managing wildlife diseases requires an understanding of disease transmission, which may be strongly affected by host population density and landscape features. Transmission models are typically fit from time-series disease prevalence data and modelled based on how the contact rate among hosts is affected by density, which is often assumed to be a linear (density-dependent transmission) or constant (frequency-dependent transmission) relationship. However, long-term time-series data is unavailable for emerging diseases, and this approach cannot account for independent effects of landscape. We developed a mechanistic model based on ecological data to empirically derive the contact rate–density relationship in white-tailed and mule deer in an enzootic region of chronic wasting disease (CWD) in Alberta, Canada and to determine whether it was affected by landscape. Using data collected from aerial surveys and GPS-telemetry, we developed empirical relationships predicting deer group size, home range size, and habitat selection to iteratively simulate deer distributions across a range of densities and landscapes. We calculated a relative measure of total per-capita contact rate, which is proportional to the number of other deer contacted per individual per unit time, for each distribution as the sum of pairwise contact rates between a target deer and all other individuals. Each pairwise contact rate was estimated from an empirical relationship developed from GPS-telemetry data predicting pairwise contact rates as a function of home range overlap and landscape structure. Total per-capita contact rates increased as a saturating function of density, supporting a transmission model intermediate between density- and frequency-dependent transmission. This pattern resulted from group sizes that reached an asymptote with increasing deer density, although this relationship was mediated by tree and shrub coverage in the landscape, such that in heavily wooded areas, the contact rate saturated at much lower densities. These results suggest that CWD management based on herd reductions, which require a density-dependent contact rate to be effective, may have variable effects on disease across a single management region. The novel mechanistic approach we employed for estimating effects of density and landscape on transmission is a powerful complement to typical data-fitting approaches for modelling disease transmission.

1. Introduction

Chronic wasting disease (CWD) is a fatal infectious prion disease of free-ranging North American cervids whose spread is thought to pose a serious threat to deer populations, which may have subsequent economic, ecological, and social consequences (Bollinger et al., 2004). CWD can be transmitted from animal to animal as well as through environmental sources, potentially including blood, saliva, faeces, or urine from diseased individuals as well as carcasses (Haley et al., 2009; Mathiason et al., 2006; Miller and Williams, 2003; Tamgüney et al., 2009). Since its initial detection in Colorado (Williams and Young, 1980), CWD has spread to wild populations in fifteen states and two Canadian provinces, many of which have ongoing research and/or management programs (CWD Alliance, 2010; Williams et al., 2002). Two broad patterns that have emerged across multiple jurisdictions are that CWD prevalence is higher in males relative to females and in mule deer (*Odocoileus hemionus*) relative to white-tailed deer (*Odocoileus virginianus*) where the species are sympatric (Farnsworth et al., 2006; Grear et al., 2006; Heisey et al., 2010; Joly et al., 2006; Miller and Conner, 2005; Osnas et al., 2009), suggesting that CWD transmission may be influenced by differences in behaviour among different host classes (i.e. species-sex classes).

Successful disease management requires reducing disease transmission such that the number of new infections created per infected host (the basic reproductive number, R_0) falls below 1 (Wobeser, 2002). Approaches to achieve this objective will depend strongly on the nature of transmission for the host–pathogen

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system in question. Culling, vaccinating, or sterilizing hosts are effective when disease transmission, specifically the contact rate among hosts, is density-dependent (hereafter "DD"; Begon et al., 2002; Lloyd-Smith et al., 2005). In contrast, if transmission is governed by the proportion of infected individuals only (known as frequency-dependent transmission, hereafter "FD"), then reducing the number of infected hosts is the only viable strategy, for example through selectively culling infected hosts (Lachish et al., 2010). While selectively culling infected deer reduces both the number of infected hosts as well as overall density (Lachish et al., 2010), it is not a feasible strategy for deer populations unless they are small, isolated, and habituated to human presence to facilitate capturing (e.g. Wolfe et al., 2004). Most management strategies for CWD to date have been based on reducing deer density through wide-scale culling or increased hunter opportunities (Williams et al., 2002). How this approach contributes to disease control requires a better understanding of how changes in density affect transmission dynamics of a host–pathogen system (Wobeser, 2002).

Additionally, DD and FD transmission represent two ends of the same continuum (Smith et al., 2009), and several authors have argued that CWD transmission should be intermediate between these two extremes (Schauber et al., 2007; Schauber and Woolf, 2003). CWD transmission occurs readily among members of a social group (Cullingham et al., 2011; Grear et al., 2010) which is typically associated with FD transmission structure (Altizer et al., 2003; Cross et al., 2005), but group size may be non-linearly related to density (McLellan et al., 2010) which may introduce some DD effects. Although studies of infectious disease transmission have traditionally focussed on how host density affects contact rates, recently there has been a greater appreciation of how landscape features may also shape disease transmission and prevalence (Ostfeld et al., 2005). Indeed, CWD prevalence has been demonstrated to be spatially structured in multiple jurisdictions (Farnsworth et al., 2005; Heisey et al., 2010; Joly et al., 2006). Spatial heterogeneity in resources may contribute to the rates of contact by locally concentrating hosts (Greer and Collins, 2008), influencing their ranging patterns and home range sizes (Kie et al., 2002; Walter et al., 2009) and altering group size (Jepsen and Topping, 2004).

Assumptions of DD versus FD transmission are typically tested for a particular host–pathogen system by statistically fitting time-series prevalence data to epidemiological models (Heisey et al., 2006; Smith et al., 2009). Such efforts have been inconclusive for CWD, likely due to its slow-spreading nature, which necessitates an extremely long-term dataset (Wasserberg et al., 2009). Therefore, in the current absence of long-term time-series prevalence data to fit to theoretical epidemiological models, assessing the influence of density and landscape features on CWD transmission may be possible using a mechanistic, bottom-up approach based on deer behaviour. Previous approaches to estimating contact rates among deer using behavioural data have been limited to pairwise contact rates for a sample of GPS-collared deer and the determination of how contact rates are influenced by spatial overlap, group membership (Schauber et al., 2007), and landscape features (Kjaer et al., 2008). However, the total contact rate must include contacts with all neighbouring deer and not just collared individuals. Tracking a sufficient number of hosts to extrapolate from pairwise to per capita total contact rates is not feasible for a large population of highly mobile hosts such as deer. Alternatively, if deer density and landscape patterns have predictable effects on home range and group sizes, home range locations, and pairwise contact rates where home ranges overlap, then these relationships can be used to assess the potential influence of changing density and landscape patterns on potential contact rates (e.g. White et al., 1995). Such a mechanistic assessment may provide a better understanding of how landscape heterogeneity mediates density-dependent and -independent effects in transmission rates, which typically is not possible when fitting statistical models to derive estimates of transmission or force of infection (Heisey et al., 2006).

In this paper, we model contact rates for simulated distributions of white-tailed and mule deer under varying densities and extents of deer habitat on the landscape. Simulated distributions were created using species-specific relationships predicting the number and sizes of deer groups from deer density, home range size and overlap from deer density and deer resource selection, and pairwise contact rates as a function of home range overlap and landscape features. We developed these relationships using data from a field study of sympatric white-tailed and mule deer in eastern Alberta, Canada, where CWD was first detected in 2005. We focused our analyses on winter, because estimates of deer density were available to derive empirical relationships, and because deer tend to aggregate on winter range (Lingle, 2003; Nixon et al., 1991), leading to contact rates considerably higher during winter (Farnsworth et al., 2006; Habib, 2010). We hypothesized that differences between white-tailed and mule deer in space use and grouping behaviour (Lingle, 2003) may lead to differences in species-specific contact rates that may account, at least in part, for the vastly different CWD prevalence rates between species.

2. Modelling disease contact rate

In epidemiological models, the change in the number of infected hosts (I) in a population over time is expressed as

$$\frac{dI}{dt} = Scpv \tag{1}$$

where S is the number of susceptible hosts, c is the contact rate, or the number of other hosts encountered per individual per unit time, p is the probability that the contact occurs with an infected host, and v is the probability that a contact between an infected and susceptible host will successfully transmit disease (Begon et al., 2002). The value of p is commonly assumed to be the proportion of hosts in the population that is infected, which implicitly assumes that infected individuals are distributed homogeneously throughout the population. The v term typically is considered to be constant for a particular host- or host class-pathogen system. Under these assumptions, differences in the transmission rate are due to the contact rate, c, or more precisely how c is related to density (Begon et al., 2002).

In following the classical approaches, DD transmission is derived by assuming c is linearly related to density, implying random mixing of hosts, whereas FD transmission assumes that c is constant or unaffected by density. However, because strictly DD- or FD-structured models are likely unrealistic descriptions of how hosts interact, it is not surprising that neither model is particularly well-supported by empirical studies (Lloyd-Smith et al., 2005; McCallum et al., 2001; Wasserberg et al., 2009). More realistic models reflecting contact rate may be represented by a general contact–density equation that allows for a wide range of relationships (Smith et al., 2009):

$$c = k\left(\frac{N^{(1-q)}}{A}\right) \tag{2}$$

In this equation, c is the total per capita contact rate (defined as the number of deer contacted per individual per unit time), N is the host population size, A is the area inhabited by the host population, and k represents an overall scaling constant particular to a host–pathogen system. Of particular consequence is q, a dimensionless scaling constant ≤ 1 that dictates the concavity of the density–contact rate relationship. DD and FD contact rates are obtained in the special cases where q is equal to 0 or 1, respectively,