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PERSPECTIVE

An epidemiological framework for chronic wasting disease in multihost communities

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Abstract

1. Many pathogens can infect several host species, which complicates the management of wildlife diseases. Even for generalist pathogens, hosts are not equally competent, and variable niche overlap between hosts leads to different exposure levels within hosts when compared with that between hosts. Hence, the processes determining spillover risk and the subsequent transmission dynamics within and between species differ.
2. Chronic wasting disease (CWD) is a contagious prion disease of the cervids detected across expanded geographic ranges over the last few decades. Multihost management has become topical with CWD detection among reindeer *Rangifer tarandus* in Europe, with an immediate spillover risk to sympatric species. Here, I argue for the use of a community epidemiological framework that distinguishes between- and within-host dynamics arising from host competence and exposure processes.
3. In CWD, host competence is mainly determined by how variants of the prion protein gene (*PRNP*) affect susceptibility. The exposure level is not only linked to the density of infected and susceptible hosts both within and between species but also to the spatiotemporal niche overlap between species and social organization within species.
4. Mule deer *Odocoileus hemionus* and white-tailed deer *Odocoileus virginianus* are highly susceptible and expected to show true multihost dynamics; however, mule deer have a higher CWD prevalence in sympatric areas, indicating only partially linked dynamics. Moose *Alces alces* are highly susceptible, but cases of CWD-infected moose are few and appear to be spillover events with subsequent epidemic die outs. Elk *Cervus canadensis* have less susceptible *PRNP* variants and low levels of prion shedding in lymphoid tissues, indicating lower contagiousness. CWD prevalence in elk is lower and appears to result from spillover and subsequent within-species emergence, which is partially independent of sympatric deer.
5. *Synthesis and applications*. Stronger awareness of the different expected CWD dynamics within and between species may facilitate effective surveillance and management. Surveillance should consider the potential lack of linked dynamics between

species when designing sampling. Multihost management can target niche overlap at different scales to limit spillover risk: (1) geographic distribution ranges, (2) density reductions in overlap zones and (3) co-use of transmission hot spots.

KEYWORDS
cervids, exposure, generalist pathogens, host competence, niche overlap, prion protein gene (*PRNP*), spillover, susceptibility

1 | INTRODUCTION

Wildlife diseases involving multiple host species pose a considerable challenge to management (Downs et al., 2019; Johnson et al., 2015; Rigaud et al., 2010; Woolhouse et al., 2001). Culling one host species may not be effective in combating wildlife diseases if there are alternative reservoir hosts (Joseph et al., 2013), and understanding the role of multiple hosts in disease dynamics is required for effective mitigation. Determining host competence (or susceptibility) is key to determining the host range and the level to which a given pathogen is actually a true multihost generalist (Becker et al., 2020). This can be challenging, as establishing a host infection is different from establishing host competence (Wilber et al., 2022). In addition, different levels of within- and between-species transmissions arise from an incomplete niche overlap and different contact networks (Barroso et al., 2023). This issue has received considerable theoretical and empirical attention, as approximately half of the pathogenic viruses and bacteria are generalists infecting more than one host (Shaw et al., 2020).

The contagious prion disease of cervids, chronic wasting disease (CWD), has been detected across expanded geographic ranges over the last few decades, with adverse effects being exerted on cervid populations and the associated economic and cultural values (Haley & Hoover, 2015; Moreno & Telling, 2018). Multihost management has become topical with CWD detection among reindeer *Rangifer tarandus* in Europe, with an immediate spillover risk to other sympatric species. CWD is typically viewed as a multihost disease of the cervids. However, the literature on CWD does not address the full complexity of how the host range affects spillover risk and subsequent (lack of) linked dynamics, which in turn affects how management views CWD. The distribution map of CWD for North America contains no information on species (National Wildlife Health Center, 2022). The mandatory surveillance of CWD in Europe during the 2018–2020 period does not differentiate cervid species and set a common target for sample sizes of the member states irrespective of the species composition of a sample (The European Commission, 2017). Here, I argue that placing CWD within a general community epidemiological framework can enhance disease management in multihost communities since exposure patterns will vary considerably between species when compared to within species. Furthermore, species variation in recruitment rates will result in different dilution levels; however, that is not the focus here.

2 | HOST COMPETENCE: *PRNP*

The only contagious prion disease among wildlife is CWD (Haley & Hoover, 2015; Moreno & Telling, 2018). Prion diseases are a group of neurodegenerative and lethal diseases associated with a type of pathogen that is fundamentally different from most other infectious agents. Cellular prion protein (PrP^{C}) is found at the highest concentration in the central nervous system (CNS) in all mammals, and infectious agents called prions are clusters of misfolded prion proteins (PrP^{Sc}). The gene encoding the prion protein (*PRNP*) determines the three-dimensional structure of the cellular prion protein, which in turn largely determines susceptibility to a given prion strain both within and between species. Therefore, host competence for prion diseases is typically inferred from the combination of (1) knowledge of *PRNP* genotype and (2) whether there are reported cases of infection. Most cervid species are susceptible to CWD based on documented infections and susceptibility inferred from *PRNP* sequences (Otero et al., 2021). The most common 'wild-type' *PRNP* refers to the original evolutionary version associated with high susceptibility to CWD. Furthermore, most species have a few other *PRNP* variants while some species do not have the wild type. Fallow deer *Dama dama* are the only known cervid species regarded as resistant to CWD based on their lack of infection when kept in captivity together with infected deer (Rhyan et al., 2011). Hence, there is an extensive focus on the role of genetics in the host range, and *PRNP* composition affects the likelihood of spillover (Arifin et al., 2020). However, the processes and risks of spillover among cervid species and the level of subsequent linked transmission dynamics in multiple species are more complex.

3 | CWD PREVALENCE IN MULTIHOST COMMUNITIES

As a basis for my arguments, I provide a systematic review of published patterns of CWD prevalence involving more than one wild host in the same area. I only considered contagious CWD and not the sporadic CWD variant observed in moose and red deer *Cervus elaphus* in Europe (Tranulis et al., 2021). The reported host ranges of CWD in North America are white-tailed deer *Odocoileus virginianus*, mule deer *Odocoileus hemionus*, elk *Cervus canadensis* and moose *Alces alces* (Moreno & Telling, 2018). Therefore, I searched

the ISI Web of Science Core Collection on 1 December 2022 using the query 'prevalence AND CWD AND (deer OR wapiti OR elk OR moose)' and screened all 139 hits for relevance (see Appendix S1 in Supporting Information). Only two of the 139 studies included all the three cervid species (Table 1) from Wyoming and Colorado (Miller et al., 2000), and South Dakota, United States (Jacques et al., 2003). Three studies involved both white-tailed and mule deer in Saskatchewan (Rees et al., 2012) and/or Alberta, Canada (Nobert et al., 2016; Smolko et al., 2021), whereas one study from South Dakota, United States, did not provide sufficient data for separate estimations (Schuler et al., 2018). No study has reported CWD prevalence in moose. One case report on CWD in wild moose was published (Baeten et al., 2007), whereas a review reported later CWD cases in Colorado and Wyoming, United States, and Canada (Moreno & Telling, 2018).

A lower CWD prevalence has been observed in elk than in deer of the genus *Odocoileus* (Race et al., 2007). CWD prevalence higher than 15% is rarely observed in elk (Monello et al., 2017), although a prevalence of up to 29% has been reported at the local scale (Sargeant et al., 2021). White-tailed deer in areas with high population densities may exhibit a high prevalence of up to 50% and are comparable to mule deer. Studies with overlapping populations have reported a higher CWD prevalence in mule deer than in white-tailed deer (Table 1). Mule deer were 2.3 times more likely to be CWD-positive than white-tailed deer in Colorado and Wyoming, United States (Miller et al., 2000), 3.7 times in Saskatchewan (Rees et al., 2012) and 4.8 times in Alberta, Canada (Smolko et al., 2021). The few studies available for comparison partially reflect the lack of an overlap in the geographic distribution of multiple cervid species in most areas.

4 | CWD DYNAMICS: COMPETENCE AND EXPOSURE

The effect of *PRNP* exerted through physiological processes largely determines host competence (see above) and strongly influences transmission, both within and between species. Nevertheless, an understanding of the more direct physiological mechanisms for transmission and spillover is limited. The competence of wild hosts of viral diseases can be inferred by detecting the shedding of live viruses (Becker et al., 2020). CWD prions are shed in the body fluids of infected deer (Davenport et al., 2018), and the level of involvement of the lymphatic system is key to shedding and contagiousness. The lower CWD prevalence observed in elk than that in deer of the genus *Odocoileus* could be explained by the lower prion levels in lymphoid tissues in elk than in deer (Race et al., 2007). The distribution of prions in lymphoid tissues in white-tailed deer is more similar to that in mule deer (Schuler et al., 2005). Furthermore, the recently documented strain variation in CWD prions adds to its complexity (Tranulis et al., 2021), but we have a limited understanding of how strain variation affects spillover and combined transmission dynamics under natural conditions.

The likelihood of transmission within and between species is a function of both susceptibility (mainly *PRNP*) and exposure; however, exposure patterns within and between species will vary, thereby decoupling the two processes. CWD can be transmitted either directly by (oral) contact or through environmental contamination (Miller et al., 2004). Within species, direct transmission is assumed most important in early stages characterized by slow epidemic growth ($R0 = 1.3–1.5$; Miller et al., 2006), with indirect transmission being increasingly important leading to more rapid epidemic growth in later stages. Various cervid species rarely have direct contact, and spillover risk is probably related to an indirect transmission route and environmental contamination. Prions can persist in the environment for several years (Miller et al., 2004). Host niche overlap and population densities (infected and susceptible) of both species likely determine the risk of exposure. The expectation is that more social species have higher within-species transmission owing to high exposure via both direct and indirect routes; however, sociality level per se likely has no impact on spillover risk from another species.

5 | MULTIHOST DYNAMICS

Using a community epidemiological framework to classify disease threats (Fenton & Pedersen, 2005), I summarized knowledge on CWD in multiple cervid species in North America (Figure 1). A key point is that spillover and subsequent within- and/or between-species transmissions are distinct processes, which lead to different pairwise CWD dynamics among species: (1) Mule deer and white-tailed deer are equally competent based on *PRNP*; that is, expected *true multihost*. These two species appear to be strongly affected by CWD (DeVivo et al., 2017; Edmunds et al., 2016). However, mule

TABLE 1 An overview of studies that reported CWD prevalence in more than one host species within the same area. Only studies involving host species in the wild are included. The 95% confidence limits are provided when available. M, males; F, females.

Location	Years	White-tailed deer	Mule deer	Elk	Reference
Colorado, Wyoming, USA	1996–1999	2.1% [0.5–3.4%]	4.9% [4.1–5.7%]	0.5% [0.001–1%]	Miller et al. (2000)
South Dakota, USA	1997–2002	0.001% [0–0.007%]	0.0% [0–0.011%]	0.0% [0–0.004%]	Jacques et al. (2003)
Saskatchewan, Canada	2002–2007	M: 0.4%; F: 0.2%	M: 1.6%; F: 0.7%		Rees et al. (2012)
Alberta and Saskatchewan, Canada	2000–2013	0.13% [0.04–0.23%]	0.69% [0.54–0.85]		Nobert et al. (2016)
Alberta, Canada	2005–2018	M: 1.1%; F: 0.3%	M: 5.4%; F: 1.5%		Smolko et al. (2021)

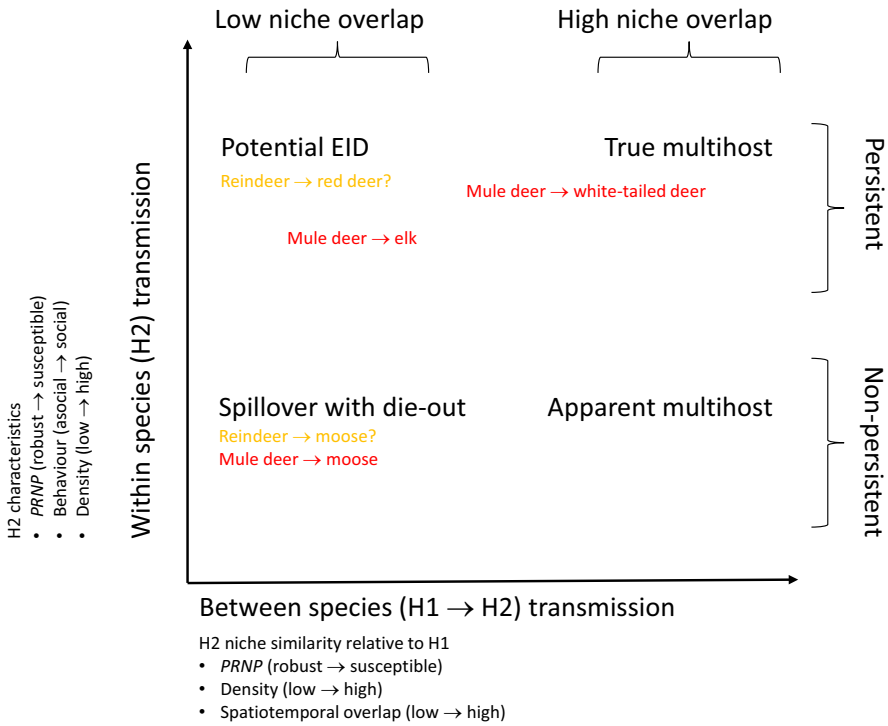

FIGURE 1 A conceptual figure illustrating chronic wasting disease (CWD) dynamics among host species in North America, and a priori assumptions regarding CWD dynamics in a multihost cervid community in Europe based on known host species traits and niche overlap. Adapting the community epidemiology framework of Fenton and Pedersen (2005). EID, emerging infectious disease; H1/H2, host 1/host2; *PRNP*, prion protein gene.

deer have a higher prevalence than white-tailed deer in sympatric areas (Table 1), which indicates lower transmission rates between than within species, making CWD dynamics only partially connected. One possibility is that mule deer have a larger group size than white-tailed deer (Lingle, 2003). The low densities of white-tailed deer populations at the northern distribution limit provide another possible explanation for their lower CWD prevalence than that of mule deer. Higher white-tailed deer recruitment rates also lead to more rapid dilution, irrespective of variations in transmission. (2) Anecdotal evidence suggests that moose was infected when using sympatric ranges to infected mule deer, but with no subsequent epidemic in moose (Baeten et al., 2007); that is, *spillover with die out*. One likely explanation is either a low population density of moose or that their asocial behaviour leads to epidemic die out, even with the susceptible wild-type *PRNP*. (3) Elk appear to have CWD dynamics that are more independent of mule deer and white-tailed deer; that is, *spillover with subsequent within-species emergence in new hosts* (Figure 1). The different *PRNP* genotypes in elk that lead to low contagiousness appear to be the main factor (Race et al., 2007); however, the role of spatial overlap in CWD dynamics has not been investigated. Elk and mule deer overlap in distribution over large areas of western United States and Canada. At high densities, elk outcompete and displace mule deer from sympatric ranges (Stewart et al., 2002), which leads to a low niche overlap at a local scale and may further contribute to their distinct CWD dynamics.

6 | MANAGEMENT AND SURVEILLANCE

A community epidemiological framework can inform surveillance and management. Even with similar *PRNP*, a partial niche overlap between species will yield different exposure patterns within and between species, resulting in only partially linked CWD dynamics between species. Therefore, caution should be taken when pooling samples across species to estimate CWD prevalence or to determine freedom from infection, as with data from the regulation for mandatory surveillance by the EU (The European Commission, 2017). In the United States and Canada, no study has analysed spillover or the relative role of within- and between-species transmission of CWD, and prevalence estimates are the only information available on (lack of) linked dynamics (Table 1). A community epidemiological framework can enable a priori assumptions regarding CWD dynamics depending on host species traits to guide further research and management (Figure 1). Thus far, this has only been built on general knowledge rather than formal analysis of seasonal niche overlap at different spatial scales. More formal modelling of spillover risk between species has been performed for the elk-to-livestock transmission risk of brucellosis in Yellowstone (Rayl et al., 2019). Such risk maps can benefit multispecies management and effectively target spillover risk at different scales of overlap: (1) At the broadest scales, limiting distribution ranges of an infected host species to modify host community composition is an option for range expansion of CWD and spillover risk. A notable case is the northward range expansion of white-tailed deer in Canada towards susceptible caribou populations (Arifin et al., 2020). Creating spatial buffer zones with targeted culling of dispersing deer, thereby keeping the densities of infected hosts at a minimum, is one option. (2) At the regional scale, reducing the population densities of different host species in overlap zones would reduce spillover risk. (3) At finer scales, hot spots for disease spillover can be managed by fencing. The recent detection of CWD among wild reindeer in Europe necessitates

urgent action to prevent spillover to sympatric species such as red deer, moose and roe deer *Capreolus capreolus*, which have considerable cultural and economic values in Europe.

AUTHOR CONTRIBUTIONS

Atle Mysterud conceived the ideas and wrote the paper.

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CONFLICT OF INTEREST STATEMENT

I declare no conflict of interest.

DATA AVAILABILITY STATEMENT

There is no data connected to this paper.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. A systematic review of studies reporting prevalence of chronic wasting disease of cervids. A search in ISI Web of Science Core Collection was performed on 1 December 2022 using the query "prevalence AND CWD AND (deer OR wapiti OR elk OR moose)" and screened all 139 hits for relevance (Supplementary Table S1). A total of 33 studies provided prevalence estimates for white-tailed deer, 23 for mule deer and 7 for elk from different areas or time periods in the same area. Only the studies in Table S1 reporting prevalence from more than one species was reported in Table 1 in the paper.
Table S1. Those with topic prevalence were considered. Wtd, white-tailed deer; Mule, mule deer.

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