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THE RELATIONSHIP BETWEEN HARVEST MANAGEMENT AND CHRONIC WASTING DISEASE PREVALENCE TRENDS IN WESTERN MULE DEER (*ODOCOILEUS HEMIONUS*) HERDS

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ABSTRACT: We analyzed retrospective data on harvest management practices and corresponding chronic wasting disease (CWD) prevalence trends in 36 western US and Canadian mule deer (*Odocoileus hemionus*) management units (units). Our analyses employed logistic regression and model selection, exploiting variation in practices within and among jurisdictions to examine relationships between harvest management and apparent prevalence (the proportion of positive animals among those sampled). Despite notable differences in hunting practices among jurisdictions, our meta-analysis of combined data revealed strong evidence that the amount of harvest was related to CWD prevalence trends among adult male mule deer in the 32 units where prevalence at the start of the analysis period was ≤5%. All competitive models included the number of male deer harvested or number of hunters 1–2 yr prior as an explanatory variable, with increasing harvest leading to lower prevalence among males harvested in the following year. Competitive models also included harvest timing. Although less definitive than the number harvested, median harvest dates falling closer to breeding seasons were associated with lower prevalence in the following year. Our findings suggest harvest—when sufficient and sustained—can be an effective tool for attenuating CWD prevalence in adult male mule deer across western ranges, especially early in the course of an epidemic. Evidence of a broad relationship between the amount of harvest and subsequent changes in CWD prevalence among adult male mule deer provides an empirical basis for undertaking adaptive disease management experimentation aimed at suppressing or curtailing CWD epidemics.

Key words: Chronic wasting disease, control, epidemiology, harvest, mule deer, *Odocoileus hemionus*, prion.

INTRODUCTION

Controlling chronic wasting disease (CWD; Williams and Young 1980), an infectious prion disease of multiple cervid species, has become a wildlife management imperative in parts of western North America and elsewhere (WAFWA 2017; Mysterud and Edmunds 2019). Without management intervention, CWD can eventually compromise the performance and resiliency of affected host populations and lead to population declines (Edmunds et al. 2016; DeVivo et al. 2017). The inherent difficulty of detecting emergent epidemics in natural systems, combined with a protracted infectious period and environmental persistence of the prion agent, probably precludes eradication once CWD becomes established in the wild (Miller et al. 2000, 2020; WAFWA 2017). Nonetheless, early management of CWD may help slow epidemic growth and environmental accumulation of prions leading to harmful population-level effects (Potapov et al. 2016; WAFWA 2017). Once prevalence (the proportion of animals infected) reaches high levels and significant environmental

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accumulation has occurred, management options may become more limited (Edmunds et al. 2016; DeVivo et al. 2017; WAFWA 2017). Consequently, there is an urgent need to identify practical management strategies that can be implemented in a long-term, sustainable manner to blunt the disease's effects on affected cervid resources (WAFWA 2017; Mysterud and Edmunds 2019).

The amount of harvest and its timing relative to breeding season have the potential to influence CWD epidemics. Theoretical modeling (e.g., Wild et al. 2011; Jennelle et al. 2014; Potapov et al. 2016) and empirical data (e.g., Wolfe et al. 2018; Miller et al. 2020) suggested that selective and nonselective removals might affect CWD dynamics, leading us to hypothesize that the amount of harvest might relate to prevalence. Because the precise nature of suggested relationships between harvest and prevalence have not been fully evaluated, we considered additional variables with potential relationship to prevalence trends. Conner et al. (2000) reported higher CWD prevalence in male deer harvested in hunts timed closer to the breeding season, leading us to hypothesize that prevalence trends could be related to harvest timing. Consequently, we also explored variables that represented this timing.

A better understanding of the relationships between harvest management practices and CWD prevalence trends may aid agencies in repurposing or complementing current management practices to address endemic CWD (WAFWA 2017; Pattison-Williams et al. 2020). Here, we report analysis of retrospective, multijurisdictional data undertaken toward an overarching goal of expediting the identification of promising harvest strategies that may curtail CWD epidemics in mule deer (*Odocoileus hemionus*). Our analyses took advantage of up to 19 yr of available data on CWD trends and corresponding hunting and herd management practices in five western US and Canadian jurisdictions to examine whether the amount and relative timing of harvest were related to apparent prevalence (the proportion of positive animals among those sampled) as an empirical basis for adaptive disease management.

MATERIALS AND METHODS

Our analyses relied on retrospective data collected by jurisdictions with different management goals, harvest strategies, and monitoring methods. To accommodate this inherent variability, we followed the general approach laid out in Anderson et al. (1999) for analyzing empirical data related to natural resource controversies. This approach has been successfully applied to other large-scale meta-analyses, for example to understand factors that affect vital rates over space and time for Northern Spotted Owls, *Strix occidentalis caurina* (e.g., Forsman et al. 2011; Dugger et al. 2016). We embraced the recommendations of Anderson et al. (1999) for workshop participation, data inclusion, and analysis protocols. Every step was transparent and documented. We used a two-phase analysis approach, wherein we first analyzed data separately for each jurisdiction, then joined the data from all jurisdictions and performed a meta-analysis. This paper focuses on the meta-analysis portion of that process; we provide details from the analysis of individual jurisdictions' data as Supplementary Material.

Overall modeling goals and approach

Our specific goals were to assemble and synthesize available long-term data on herd and harvest management and CWD prevalence trends from cooperating western North American jurisdictions, then analyze those data to identify whether there were harvest practices showing evidence of association with reducing, stable, or increasing trends in CWD prevalence. In contrast to theoretical modeling or prospective experimental exercises, our approach relied on data gathered over nearly two decades from in situ management and disease monitoring programs.

Five agencies participated: Alberta Environment and Parks, Colorado Parks and Wildlife, Nebraska Game and Parks, Utah Division of Wildlife Resources, and Wyoming Game and Fish Department. We refer to these respective states and province collectively as "jurisdictions" throughout. Representatives from each agency attended workshops, supplied relevant data, and reviewed analysis results.

Data and areas included in analyses

Our analyses focused on mule deer because the most comprehensive data were available for this species. We summarized and compared data by spatially defined hunting management units as

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TABLE 1. Summary of the temporal and spatial distribution of harvest and animal data used in a meta-analysis of harvest (by hunting) management and chronic wasting disease prevalence trends for adult male mule deer (*Odocoileus hemionus*) harvested from management entities (units) in western Canadian (Alberta) or USA (Colorado, Nebraska, Utah, Wyoming) jurisdictions, 1999–2017.

Jurisdiction	Years[a]	No. years[a]	No. units	No. deer sampled (total)
Alberta	2006–16	12	11	7,763
Colorado	2002–17	16	7	15,634
Nebraska	2002–12	11	6	10,813
Utah	2006–17	12	3	2,809
Wyoming	2002–17	16	9	6,899

[a] The range and number of years listed reflect the time period covered by available chronic wasting disease surveillance data and resulting annual prevalence estimates. Harvest data for up to the prior 3 yr were used to populate "lagged" variables in logistic regression analyses.

defined by respective jurisdictions (hereafter unit). We limited analyses to data from adult (≥2 yr old) male mule deer harvested by hunters because insufficient data were available for females and yearling males; adult male deer were well represented in data from all five jurisdictions. Apparent prevalence in this demographic group is readily measured, relatively high, and shows measurable changes and trends through time correlating with underlying epidemic dynamics (Miller et al. 2020; Miller and Wolfe 2021).

Following the recommendation that management strategies should be evaluated for ≥10 yr (WAFWA 2017), we limited analyses to units with ≥10 yr of prevalence data. The timing of CWD detection and availability of surveillance data during 2002–17 determined the range and number of years covered by our analyses (Table 1). Harvest data 1 or 2 yr earlier (2000–16) were used to populate variables in logistic regression meta-analyses, as shown soon. We further assumed that a sampling effort yielding a sum of ≥100 samples over multiple 3-yr periods during 2002–17 was necessary. From the five jurisdictions, 36 units met these criteria (Table 1, Fig. 1, and Supplementary Material Table S1). The 36 units ranged in size from 455 to 20,221 km^2, distributed across a broad geographic region in which climate, topography, vegetation, and elevation varied widely, as did population size, amount of harvest, hunting season timing, and the likely duration of CWD occurrence (Figs. 1–3 and Supplementary Material Table S1 and Fig. S1).

Annual data used included the number of adult male deer harvested, number of hunters, estimated population size, and adult sex ratios in each unit (Supplementary Material Table S2). Data on date harvested, date submitted for testing, and laboratory result (positive or not detected) were assembled for individual harvested adult male mule deer (n=43,918; Supplementary Material Table S2). Given the retrospective nature of our analyses, we acknowledge some variation in data collection methods among participating jurisdictions (see Supplementary Material Table S2 for data collection methods). All estimates of apparent CWD prevalence (=no. positive/total no. sampled) were annual and based on the corresponding annual period (August–January; Supplementary Material Fig. S1) when hunting occurred.

Basis for harvest and timing variables

Exploratory variables were chosen largely on the basis of previous research suggesting that the amount of harvest might relate to trends in CWD prevalence. Unit- and year-specific data included harvest variables, such as the number of male deer harvested and the number of hunters. We also derived variables that were a combination of harvest variables (e.g., change in harvest) or a combination of a harvest variable and population estimate (e.g., hunter effort; Table 2). In general, these derivative variables represented harvest or hunter or license numbers relative to herd size. Because of the large variation in units and the size of mule deer herds (Supplementary Material Table S1), we included relative harvest variables to explore whether harvest and hunting pressure per animal may be more relevant than absolute measures.

In addition to variables describing the amount of harvest (harvest variables), we included variables that represented the timing of harvest. We used CWD sample submission date to approximate timing of harvest. We defined median day as the day (expressed as a number out of 365) when 50% of all sampled deer were harvested within a year and also calculated the day when 90% of all harvest had occurred.

Not all jurisdictions had the data required to generate each harvest variable originally considered, so we made adjustments to accommodate limitations to the extent possible. See Supplementary Material for additional details on variables used in our analyses.

Analysis approach

Because the CWD test result was a binary response variable (positive or not), we used logistic regression models for these analyses (Agresti 2007; Hosmer et al. 2013). Note that CWD prevalence refers to the proportion of

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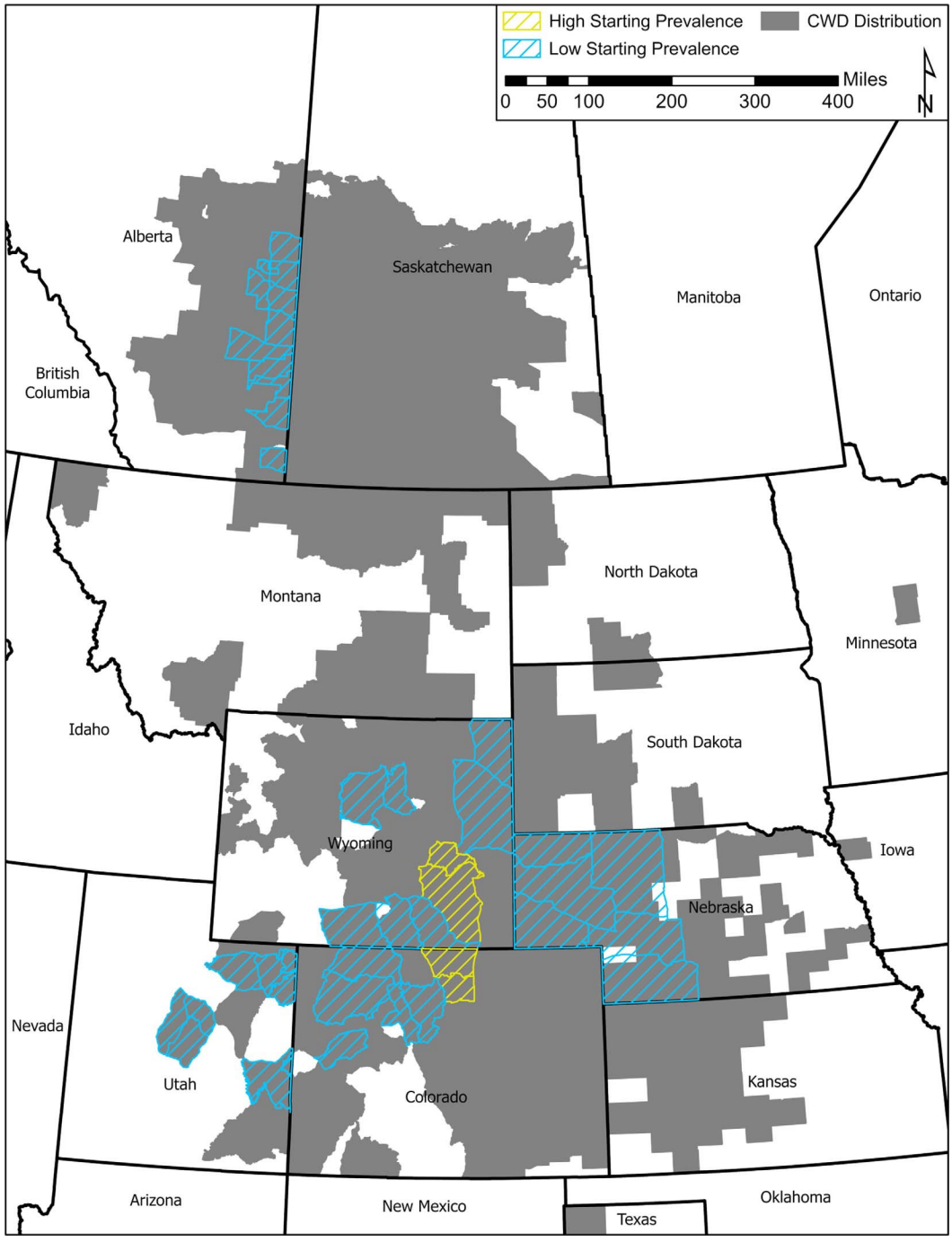


FIGURE 1. Locations of 36 western Canadian or US mule deer (*Odocoileus hemionus*) herd or management units (*Units*) included in meta-analysis of harvest (by hunting) management and chronic wasting disease (CWD) prevalence trends during 2002–17. For the meta-analysis, we distinguished units with relatively low prevalence ($\leq$5%; n=32) from those with much higher prevalence ($\geq$11%; n=4) at the beginning of respective analysis periods. See text and Supplementary Material Table S1 for additional details. Underlying CWD distribution is adapted from an online map maintained by the US Geological Survey (2020) and augmented by updated jurisdictional data.

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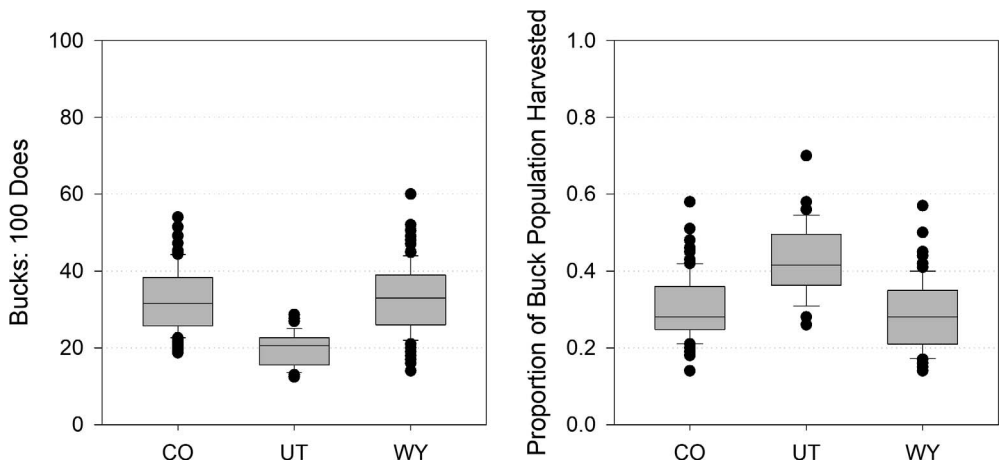


FIGURE 2. Box plots depicting variation in male:female (commonly termed buck:doe; bd) ratios and proportion of males harvested (*propbharv*; estimated as the number of males harvested divided by the estimated number of males preharvest) across jurisdictions. Estimates of the proportion of males harvested are shown only for Colorado (CO), Utah (UT), and Wyoming (WY). Alberta and Nebraska had too few bd data to include in this aspect of our analyses.

samples that were positive, which is the average of the predicted probabilities, also called sample or empirical logit (Agresti 2007). We ran all analyses in R with the *glm* or *glmer* functions (R Core Team 2018). For all model selection, we used an information-theoretic approach (Burnham and Anderson 2002) to rank candidate models and select an appropriate model. We used Akaike's information criterion (AIC; Akaike 1973) to rank models and ΔAIC and model weights to evaluate and select "top" models (Burnham and Anderson 2002). We regarded models with ΔAIC≤2 as competitive with the top model (ΔAIC=0).

Cross-jurisdiction meta-analysis

We merged data sets from all five jurisdictions for the meta-analysis. The response variable was CWD prevalence among harvested adult male mule deer. We began model construction for the meta-analysis by reviewing the results from individual jurisdictions (see Supplementary Material and Tables S3–S5) to help us decide which variables to carry forward. In addition to looking at model selection results and output from top models, we considered graphs of distributions of harvest variables, temporal patterns of harvest variables, relationships between prevalence and each harvest variable, correlations among harvest variables, and temporal patterns. Repeating a correlation analysis for the combined data revealed some strong correlations among lagged and cumulative harvest variables and among several other harvest variables (Supplementary Material Fig. S2), which allowed us to avoid using correlated variables in the same model.

The key features of our meta-analysis approach included: 1) carrying forward the number of males harvested, number of hunters (or licenses), change in male harvest, and median day; 2) summing values from the prior 1 and 2 yr for a 2-yr cumulative effect; 3) adding three timing variables (described soon); 4) modifying the approach for calculating proportion of males harvested and hunter effort to standardize these parameters across jurisdictions; 5) conducting separate analyses for 32 units that started with low prevalence (<5%) and for the four units that entered with high prevalence (≥11%), and 6) employing a mixed model with *Unit* and *Year* (slope) modeled as random effects where possible. Detailed rationales and explanations follow.

Given interjurisdictional differences in deer hunting seasons (Supplementary Material Fig. S1), we used the median date of harvest to represent the timing when the majority of harvest occurred. We also developed two new variables (Table 2) to test hypotheses more explicitly about timing of harvest relative to breeding season (Fig. 3). One variable (*pkrutto50*) captured the difference in days between local peak breeding (Julian Day 329 for Alberta, Day 324 for other jurisdictions; Anderson 1981) and the median of annual harvest. The other variable (*pkrutto90*) captured the difference between peak breeding and the day when 90% of annual harvest was achieved.

Alberta and Nebraska units did not have adequate estimates of male:female ratios to estimate male population size as needed to

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TABLE 2. Variables used in meta-analysis of harvest (by hunting) management and chronic wasting disease prevalence trends during 2002–17 for adult male mule deer (*Odocoileus hemionus*) harvested from western Canadian or United States jurisdictions.

Variable	Description	Variable name
No. male deer (bucks) harvested	Estimated from harvest surveys, lagged 1 yr (i.e., from the prior year)	*bharvno1*
Change in harvest	Number of bucks harvested this year (t) minus the number of bucks harvested the prior year ($t-1$), lagged 1 yr (i.e., difference from the prior year)	*chngharv1*
Active no. licenses[a]	Estimated from harvest surveys, lagged 1 yr (i.e., from the prior year)	*hunter1*
Proportion of male deer (bucks) harvested[b]	Number of bucks harvested/estimated population size just before hunting seasons, lagged 1 yr (i.e., from the prior year)	*propbharv1*
Hunter effort	Number of licenses sold/estimated population size just before hunting seasons, lagged 1 yr (i.e., from the prior year)	*hunteff1*
Cumulative harvest	Sum of the number of bucks harvested 1 or 2 yr before the reference year	*bharvno1plus2*
Cumulative proportion harvest	Sum of proportion of bucks harvested 1 or 2 yr before the reference year	*propbharv1plus2*
Cumulative hunters	Sum of number of hunters 1 or 2 yr before the reference year	*hunter1plus2*
Cumulative hunter effort	Sum of hunter effort 1 or 2 yr before the reference year	*hunteff1plus2*
Median day of harvest	Julian day when 50% of all samples were submitted each year, lagged 1 yr (i.e., from the prior year)	*day50.1*
Difference between peak breeding season (rut) and median day of harvest	Difference (in days) between Julian day of peak rut[c] and Julian day when 50% of all samples were submitted each year, lagged 1 yr (i.e., from the prior year)	*pkrutto50.1*
Difference between peak breeding season (rut) and 90% day of harvest	Difference (in days) between Julian day of peak rut[c] and Julian day when 90% of all samples were submitted each year, lagged 1 yr (i.e., from the prior year)	*pkrutto90.1*

[a] Estimated from number of licenses sold, also called the number of hunters afield.

[b] Every jurisdiction except Alberta estimated postharvest population size. To estimate prehunt population size for these jurisdictions, we added the total number of males, females, and fawns harvested to the posthunt population size.

[c] Estimated day of peak breeding adjusted for local differences reflected in Figure 3 and the text.

standardize harvest. Consequently, we used the total prehunt population size by unit as the denominator for proportion of males harvested and hunter effort to standardize harvest pressure (no. males harvested/prehunt population size) and hunter pressure (no. hunters/prehunt population size) for all jurisdictions.

We anticipated potential differences in responses depending on where on the generalized epidemic curve measurements began (Miller et al. 2000, 2020; WAFWA 2017). Graphing the starting CWD prevalence for all units showed a clear breakpoint: 32 units had entered the study at relatively low prevalence (<5%), but four units entered at much higher prevalence (≥11%; Fig. 4). We used ≥5% as the nominal threshold (Fig. 4).

Because the low-prevalence group included 32 units, we used a mixed effects model, with starting prevalence (intercept for each unit) and the linear relationship between CWD prevalence and year (slope for each unit) as a random effect. In doing so we reduced the number of parameters in the models from 64–66 to 4–6. The real strength of modeling unit and year as random effects is that inferences are more general (Zar 2010), extending beyond the 32 low-prevalence units we sampled to adult male mule deer in any area represented by the distribution of starting prevalences and changes through time. We could not model *Unit* and *Year* as random effects for the high-prevalence group because four units were an insufficient basis for robust estimates of mean and (especially) variance of a distribution (random effects generally need ≥10 units; Efron and Morris 1977; Burnham and White 2002). We note that modeling *Unit* and *Year* as random effects is heuristically the same as the base model with an interaction between *Unit* and *Year* (e.g., $logit(CWD\ prev) = Unit + Year + Unit \times Year$).

Similar to the analysis approach for individual jurisdictions (see Supplementary Material), we

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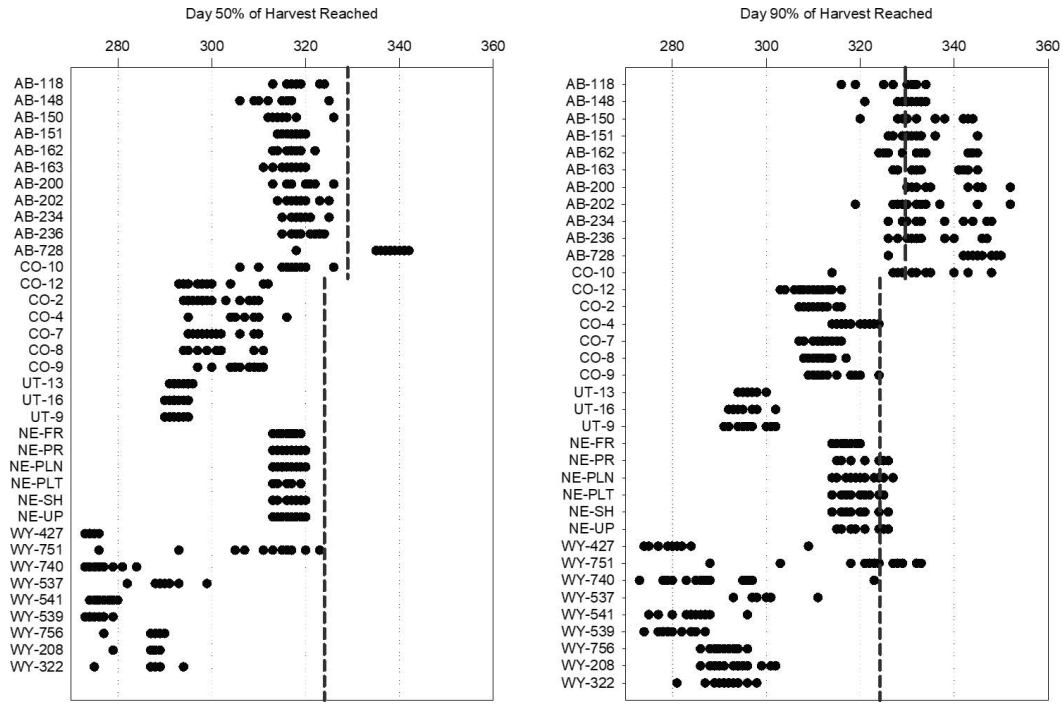


FIGURE 3. Relative timing of harvest for adult male mule deer (*Odocoileus hemionus*) taken by hunters in the western Canadian or US management units during 1999–2016. We used the median day (50% of harvest reached) and the day most of the harvest (90%) was reached to generate harvest variables for our individual jurisdiction analyses or meta-analysis of chronic wasting disease prevalence trends. Points represent data for individual years; no trend across years should be inferred. For reference, 1 October~275, 1 November~305, 1 December~335. The dashed line demarks the estimated peak mule deer breeding date in each jurisdiction. See Supplementary Material Table S1 for details on individual units. AB=Alberta, Canada; CO=Colorado; NE=Nebraska; UT=Utah; WY=Wyoming.

used a sequential process for model development (Nichols et al. 1997), adding harvest and timing variables (Table 2) to the base model. For both the mixed- and fixed-effects models, we followed the same procedure as for individual jurisdictions. That is, we added each harvest variable with a 1-yr lag or a cumulative 1- and 2-yr lag (Table 2) to the base model; we constructed a model wherein the harvest variable replaced year (e.g., *logit*(*CWD prev*)=*Unit*×*hunter*); and, for the top model(s), we added the top timing variable(s) to evaluate the potential combined effects from harvest pressure and timing on CWD prevalence.

Finally, in analyzing the four units with high starting prevalence, we recognized that management histories since 2000 differed between the two Colorado units (intensively managed for CWD suppression during 2000–06) and the two Wyoming units (no directed CWD management) and that patterns in the relationship between CWD prevalence and harvest pressure also appeared to be different. To account for this, we modeled all harvest pressure variables with an interaction between *Unit* and the variable. We modeled harvest timing variables with and without an interaction with *Unit* because the pattern in timing variables was less clear.

RESULTS

Cross-jurisdiction meta-analyses

Amount and timing of harvest showed relationships to CWD prevalence trends among male mule deer in the 32 units, where starting prevalence was ≤5%. All four competitive models (within 2 ΔAIC units of the top model) included the number of male deer harvested or number of hunters the prior 1 yr or 1–2 yr as an explanatory variable (Table 3 and Supplementary Material Table S6): increasing hunter and harvest numbers led to lower prevalence in the following year (range

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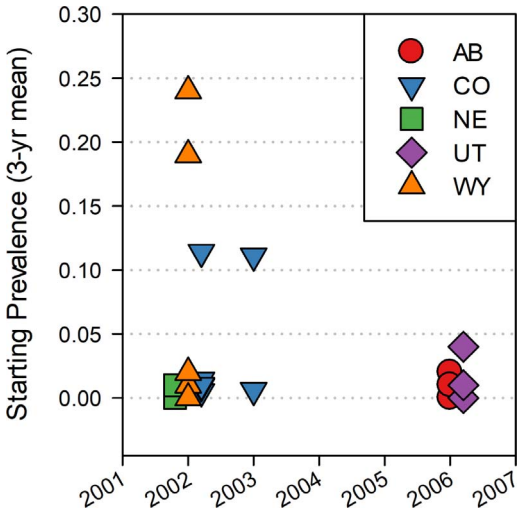


FIGURE 4. Chronic wasting disease (CWD) prevalence among harvested adult male mule deer (*Odocoileus hemionus*) in the 36 western Canadian or US management units estimated at the beginning of the unit's respective analysis period (2002–06). Visual inspection revealed a clear break separating 32 units with starting prevalence ≤5% from four units with starting prevalence ≥11%. AB=Alberta, Canada; CO=Colorado; NE=Nebraska; UT=Utah; WY=Wyoming.

of β values –0.043 to –0.218 and $P \leq 0.023$; Supplementary Material Table S7). All four competitive models also included timing of harvest: median harvest date closer to peak breeding date led to lower prevalence in the following year (Table 3), although significance of the associated β values varied (P=0.041–0.060). The four competitive models collectively accounted for ~70% of the model weight among the 15 random effect (RE) models analyzed. The base model (*UnitRE-YearRE*) was uncompetitive (ΔAIC=6.68; model weight ~0.01).

Relationships were somewhat less definitive in the four herds with high starting prevalence (Table 3 and Supplementary Material Tables S8 and S9). The three competitive fixed-effects models included the cumulative number of hunters (instead of actual harvest) in the prior 2 yr—interacting with *Unit*—as an explanatory variable. Models with cumulative number of hunters collectively accounted for ~86% of the overall explanatory weight among the 18 fixed-effects models. However, the interaction resulted in different slopes for the four units, and increasing cumulative hunting pressure led to lower prevalence only in one Wyoming herd (Supplementary Material Table S9). Although the nominally best model (ΔAIC=0.03 above the next) did not include timing, the second and third best models included harvest timing (Table 3 and Supplementary Material Table S8): later harvest led to lower prevalence in the following year, the same representation as for the lower prevalence units. The base model (*Unit*×*Year*) was uncompetitive (ΔAIC=17.97; model weight ~0).

We used β values from the top model for mule deer herds (*Units*) with low starting prevalence (*UnitRE+YearRE+bharvno1+pkrutto50.1*; Table 3) to predict prevalence at different levels of male harvest. We used mean values for *Unit*, *Year*, and *pkrutto50.1*, and a harvest level of 1,000 males for the status quo harvest. For every 100 additional males harvested, the estimated effect was a 2% decrease in CWD prevalence. That is, in year t, prevalence the following year (year t+1) would be about 0.98 times (=2%) lower than the prevalence expected under status quo harvest (e.g., 4.9% vs. 5%), or 0.81 times (19%) lower (e.g., 4.1% vs. 5%) for every 1,000 additional males harvested. Compared with harvest amount, timing had a smaller but additive estimated effect, as illustrated in Figure 5.

DISCUSSION

An overarching association between mule deer harvest management practices and CWD prevalence trends among adult male deer emerged from our meta-analysis despite notable differences in hunting practices across five jurisdictions. The top models from our meta-analysis all included harvest variables (either the number of male deer harvested or the number of hunters) with significant negative slopes, thereby providing strong evidence of a negative relationship between the amount of harvest or hunting pressure and

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TABLE 3. Model selection results for meta-analysis of harvest (by hunting) management and chronic wasting disease (CWD) prevalence trends during 2002–17 for adult male mule deer (*Odocoileus hemionus*) harvested from western Canadian or USA herds (*Unit*). All variables were lagged 1 yr, and the cumulative total from lags of 1+2 yr (i.e., *1* or *1plus2* at the end of the variable name indicates the number of years the variable was lagged). For the 32 units with low initial CWD prevalence (≤0.05), we used random effects (RE) to model the intercept (*UnitRE*) and slope (*YearRE*). Akaike's information criterion (AIC) was used to rank models; models with ΔAIC≤2 were considered competitive with the top model (ΔAIC=0). Only models with model weight ≥0.01 are shown. See Supplementary Material for model descriptions and the full set of model selection results.

Model	*K*	AIC	ΔAIC	Model weight
Units with ≤0.05 initial CWD prevalence (*n*=32)				
UnitRE+YearRE+bharvno1+pkrutto50.1	6	7,837.2	0.00	0.29
UnitRE+YearRE+bharvno1plus2+pkrutto50.1	6	7,838.5	1.33	0.15
UnitRE+YearRE+hunter1+pkrutto50.1	6	7,838.6	1.39	0.15
UnitRE+YearRE+hunter1plus2+pkrutto50.1	6	7,839.2	1.99	0.11
UnitRE+YearRE+bharvno1	5	7,839.44	2.27	0.09
UnitRE+YearRE+hunter1	5	7,840.3	3.09	0.06
UnitRE+YearRE+bharvno1plus2	5	7,840.86	3.69	0.05
UnitRE+YearRE+hunter1plus2	5	7,841.0	3.81	0.04
UnitRE+YearRE+huntereff1plus2	5	7,843.2	6.03	0.01
UnitRE+YearRE	4	7,843.9	6.68	0.01
UnitRE+YearRE+chngbharv1	5	7,843.90	6.73	0.01
UnitRE+YearRE+huntereff1	5	7,845.0	7.78	0.01
Units with >0.05 initial CWD prevalence (*n*=4)				
Unit×Year+Unit×hunter1to2	12	4,791.07	0.00	0.36
Unit×Year+Unit×hunter1to2+pkrutot50.1	13	4,791.10	0.03	0.36
Unit×Year+Unit×hunter1to2+Unit×pkrutot50.1	16	4,792.92	1.85	0.14
Unit×Year+Unit×hunter1	12	4,793.30	2.23	0.12
Unit×Year+Unit×bharvno1to2	12	4,798.49	7.42	0.01

changes in apparent CWD prevalence among adult male mule deer in subsequent years. The data underlying these relationships came from mule deer herds in 32 management units entering the analysis period with prevalence <5%. Apparent prevalence had declined or remained essentially unchanged in some of these herds, whereas in others, prevalence had increased—in some cases dramatically—over the span of 11–16 yr (Supplementary Material Table S1). Our observations complement and extend key outcomes from recent analyses that showed similar inverse relationships between hunting pressure and CWD prevalence in Colorado mule deer herds on a more local scale (Miller et al. 2020).

The modest annual effects on prevalence estimated from our analyses may be difficult to discern in the short term, as anticipated previously (Conner et al. 2007; WAFWA 2017). The field observations reported here appear consistent with theoretical modeling outcomes, wherein effects of selective or nonselective removals on CWD prevalence trends accrue over several decades (e.g., Wild et al. 2011; Potapov et al. 2016). Although driving large prevalence reductions in the short term likely would require substantial increases in harvest, we believe it encouraging that modest increases in harvest might be sufficient to slow epidemic growth or stabilize prevalence in some areas. Moreover, sustaining harvest at an adequate level over time should have cumulative effects toward stabilizing or lowering prevalence (Fig. 5). Having data-driven estimates of such effects should help adjust expectations of policymakers and constituents for in situ responses to management efforts. The cumulative effect of sustained male harvest may explain apparent lack of epidemic growth in two of the three Utah herds compared with most others (Supple-

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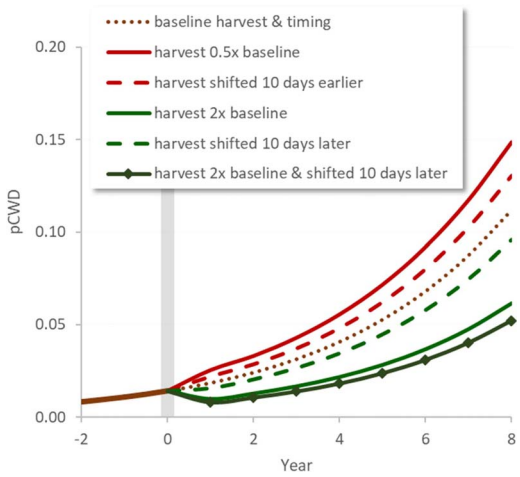


FIGURE 5. Chronic wasting disease (CWD) prevalence trends projected with β values from the top model for mule deer (*Odocoileus hemionus*) herds with low starting prevalence. Trend lines illustrate the relative influence of changes in annual harvest amount (solid lines) or timing (dashed lines) beginning at Year 0 (vertical gray bar) compared with maintaining baseline harvest (dotted line). Projected effects of halving (red; above dotted line) or doubling (green; below dotted line) harvest amount were larger than for shifting median harvest 10 days earlier (red) or later (green). The relatively small but additive effect of increased harvest shifted 10 days later is also shown for comparison (darker green with diamonds). Baseline values: *bharvno1*=3,000; *pkrutto50.1*=17.5.

mentary Material Table S1). That is, the harvest of male mule deer in Utah was proportionally greater on average than in Colorado or Wyoming (with concomitant lower male:female ratios; Fig. 2), suggesting that harvesting more males helped attenuate increases in apparent CWD prevalence in Utah.

The potential effects of harvest timing on CWD prevalence patterns may seem less intuitive to managers than those of harvest magnitude. For jurisdictions that limit mule deer harvest to periods well in advance of the breeding season (e.g., Fig. 3 and Supplementary Material Fig. S1), focusing harvest closer to the mule deer breeding season—shortly before, during, shortly after—could help lower prevalence among males harvested in subsequent years. This strategy would be expected to maximize harvest of the prime age class males that harbor disproportionately high prevalence (Miller and Conner 2005; Miller et al. 2008) by exploiting their general vulnerability to harvest as breeding commences. Moreover, these effects also could be partially selective, because infected male mule deer appear more vulnerable to harvest (Conner et al. 2000; DeVivo et al. 2017). Timing effects were included in models best explaining prevalence patterns across the 32 study units with low starting prevalence. The significant positive slopes on the timing variable (*pkrutto50.1*; Supplementary Material Table S7) common to the top models from our meta-analysis suggest applying harvest closer to the breeding season would be potentially beneficial in helping curb epidemic growth. We interpret this as evidence that timing can complement the amount of harvest in affecting changes in CWD prevalence. From a practical management standpoint, our data suggest that shifting the timing of harvest seems unlikely to substitute for sustaining or increasing the amount of harvest (Fig. 5). Rather, for any given harvest prescription, shifting the timing of male harvest toward the breeding season may offer the most efficient way to increase harvest of older male deer.

In addition to direct prospective assessments, the indirect influences of male harvest on subsequent CWD prevalence trends among adult females warrant evaluation (either by antemortem testing or harvest sampling) where feasible (e.g., Wolfe et al. 2018; Miller et al. 2020; Miller and Wolfe 2021). Moreover, we only assessed male harvest, but the effects of female harvest (resulting in a density reduction) on CWD prevalence trends also need to be evaluated. At a given male:female ratio, reducing the overall abundance also reduces the density of adult males in a unit. Conversely, increasing male harvest may not drive a desired reduction in CWD prevalence or in the total number of infected deer present on the landscape if abundance is allowed to increase. Finally, stochastic events such as severe winter or drought conditions, hemorrhagic disease epizootics, or periods of unusually high or low fawn recruitment could lead to sharp reductions or increases in overall

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deer abundance and significant changes to the age structure of an infected population (and perhaps apparent prevalence; Miller and Wolfe 2021). It follows that it will be worthwhile to gather data in a manner affording opportunities to assess the effects of large stochastic perturbations on subsequent CWD prevalence trends.

Given adequate sampling, repeated meta-analyses should provide more knowledge than analyzing each jurisdiction separately. In a recent paper, Nichols et al. (2019) contended that most ecologic investigations are viewed as standalone studies, with inadequate attention devoted to accumulation of evidence and subsequent knowledge that come from meta-analyses and repeated analyses. Our multi-jurisdictional approach includes a much wider range of management types, such as season dates and harvest pressures, than would be possible within a single jurisdiction in an experimental framework. Jurisdictions manage deer hunting on the basis of biological and social preferences. Herd performance and hunting traditions vary widely in western North America. Evaluation of harvest effects on CWD prevalence seems sufficiently important to warrant carefully designed monitoring, field experimentation, and meta-analyses. Finally, our analysis was retrospective. No matter how well designed or spatially and temporally extensive, such endeavors can only define relationships. Field experimentation remains necessary to determine whether increased harvest can drive a corresponding decline in CWD prevalence among male mule deer.

Beyond yielding findings that emphasize the potential utility of harvest in suppressing CWD prevalence in mule deer and perhaps other susceptible free-ranging hosts, our approach to iterative, interjurisdictional comparison and analyses of field data will, one hopes, serve as an example of how other wildlife disease problems might be approached. We view retrospective analyses such as this particularly valuable in providing insights into disease systems wherein the necessary timeframes for gaining such insights may span decades. Our analyses revealed evidence of harvest practices probably having some effect on observed prevalence trends. The harvest regimens in use were not consistently applied over the entire period and, for the most part, were not explicitly invoked as planned CWD management actions. Nonetheless, projections from our analyses do suggest that sustaining harvest at an increased level over time will have cumulative effects toward limiting prevalence. This should be tested by field experimentation, ideally over a variety of units with different environmental conditions and overall management. Results from such field experimentation, analyzed in a meta-analysis framework, would provide powerful guidance for future CWD management. Meta-analysis of available data could then serve as a foundation for further progress toward controlling important wildlife diseases—including CWD—through iterative, experimentally based, adaptive management.

Management implications

The apparent relationships between harvest and prevalence revealed by our analyses merit consideration by wildlife managers and policymakers across mule deer range wherever CWD has been detected. Inferences about harvest effects seem most immediately applied to CWD suppression in mule deer herds with relatively low prevalence given the available data, but implementing and evaluating harvest-based suppression strategies regardless of starting prevalence probably will be informative. Increasing male harvest reduces male and overall deer abundance, density, and the number of deer infected and changes male age structure, all of which may influence prevalence and incidence trends in a manner akin to selective removal, by focusing mortality on the most heavily infected demographic (Wild et al. 2011; Jennelle et al. 2014; Potapov et al. 2016). The effects of specific strategies such as "antler point restrictions," which focus all harvest pressure on adult males, also could be analyzed given sufficient data. Minimally, harvest management decision-making should

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consider potential effects on CWD dynamics—for better or worse—moving forward.

The limitations of our data and analyses underscore the value of sustained sampling under guidance of a study design, the importance of collectively combining evidence from smaller studies, and the necessity in field-based experiments to test the effect of harvest manipulations on CWD prevalence. Only a proportion of units sampled by each jurisdiction met minimum sample size assumptions for this analysis; even these suffered from data gaps and compromises because of low sample size. Future meta-analyses can be enhanced by defining analysis goals and designing a corresponding sampling scheme. When resources are limited, surveying fewer sampling units more intensively may offer the precision needed to detect trends within an area (Thompson et al. 1998; MacKenzie and Royle 2005; WAFWA 2017). Therefore, we recommend selecting representative target units and sampling them at regular intervals to meet sample size requirements. Additionally, we recommend agencies collect data on male:female ratios for target areas so the proportion of males harvested can be estimated. Finally, we note that this approach is not intended for detecting spatial spread of CWD, which requires a different monitoring design.

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SUPPLEMENTARY MATERIAL

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LITERATURE CITED

Agresti A. 2007. *An introduction to categorical data analysis*. 2nd Ed. John Wiley & Sons, New York, New York, 400 pp.

Akaike H. 1973. Information theory as an extension of the maximum likelihood principle. In: *Proceedings of the second international symposium on information theory*, Petrov BN, Csaki F, editors. Akademiai Kiado, Budapest, Hungary, pp. 267–281.

Anderson AE. 1981. Morphological and physiological characteristics. In: *Mule and black-tailed deer of North America*, Wallmo OC, editor. University of Nebraska Press, Lincoln, Nebraska, pp. 27–97.

Anderson DR, Burnham KP, Franklin AB, Gutiérrez RJ, Forsman ED, Anthony RG, White GC, Shenk TM. 1999. A protocol for conflict resolution in analyzing empirical data related to natural resource controversies. *Wildl Soc Bull* 27:1050–1058.

Burnham KP, Anderson DR. 2002. *Model selection and multimodel inference*. 2nd Ed. Springer-Verlag, New York, New York, 488 pp.

Burnham KP, White GC. 2002. Evaluation of some random effects methodology applicable to bird ringing data. *J Appl Stat* 29:245–264.

Conner MM, McCarty CW, Miller MW. 2000. Detection of bias in harvest-based estimates of chronic wasting disease prevalence in mule deer. *J Wildl Dis* 36:691–699.

Conner MM, Miller MW, Ebinger MR, Burnham KP. 2007. A meta-BACI approach for evaluating management intervention on chronic wasting disease in mule deer. *Ecol Appl* 17:140–153.

DeVivo MT, Edmunds DR, Kauffman MJ, Schumaker BA, Binfet J, Kreeger TJ, Richards BJ, Schätzl HM, Cornish TE. 2017. Endemic chronic wasting disease causes mule deer population decline in Wyoming. *PLoS One* 12:e0186512.

Dugger KM, Forsman ED, Franklin AB, Davis RJ, White GC, Schwarz CJ, Burnham KP, Nichols JD, Hines JE, Yackulic CB, et al. 2016. The effects of habitat, climate and barred owls on long-term demography of northern spotted owls. *Condor Ornithol Appl* 118: 57–116.

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Edmunds DR, Kauffman MJ, Schumaker BA, Lindzey FG, Cook WE, Kreeger TJ, Grogan RG, Cornish TE. 2016. Chronic wasting disease drives population decline of white-tailed deer. *PLoS One* 11:e0161127.

Efron B, Morris C. 1977. Stein's paradox in statistics. *Sci Am* 236:119–127.

Forsman ED, Anthony RG, Dugger KM, Glenn EM, Franklin AB, White GC, Schwartz CJ, Burnham KP, Anderson DR, Nichols JE, et al. 2011. Population demography of Northern Spotted Owls. *Studies in Avian Biology 40*. University of California Press, Berkeley, California, 106 pp.

Hosmer DW Jr, Lemeshow S, Sturdivant RX. 2013. *Applied logistic regression*. 3rd Ed. John Wiley & Sons, New York, New York, 436 pp.

Jennelle CS, Henaux V, Wasserberg GB, Thiagarajan B, Rolley RE, Samuel MD. 2014. Transmission of chronic wasting disease in Wisconsin white-tailed deer: implications for disease spread and management. *PLoS One* 9:e91043.

MacKenzie DI, Royle JA. 2005. Designing occupancy studies: general advice and allocating survey effort. *J Appl Ecol* 42:1105–1114.

Miller MW, Conner MM. 2005. Epidemiology of chronic wasting disease in free-ranging mule deer: Spatial, temporal, and demographic influences on observed prevalence patterns. *J Wildl Dis* 41:275–290.

Miller MW, Runge JP, Holland AA, Eckert MD. 2020. Hunting pressure modulates prion infection risk in mule deer herds. *J Wildl Dis* 56:781–790.

Miller MW, Swanson HM, Wolfe LL, Quartarone FG, Huwer SL, Southwick CH, Lukacs PM. 2008. Lions and prions and deer demise. *PLoS One* 3:e4019.

Miller MW, Williams ES, McCarty CW, Spraker TR, Kreeger TJ, Larsen CT, Thorne ET. 2000. Epizootiology of chronic wasting disease in free-ranging cervids in Colorado and Wyoming. *J Wildl Dis* 38: 676–690.

Miller MW, Wolfe LL. 2021. Inferring chronic wasting disease incidence from prevalence data. *J Wildl Dis* 57:718–721.

Mysterud A, Edmunds DR. 2019. A review of chronic wasting disease in North America with implications for Europe. *Eur J Wildl Res* 65:26.

Nichols JD, Hines JE, Blums P. 1997. Tests for senescent decline in annual survival probabilities of common pochards, *Aythya ferina*. *Ecology* 78:1009–1018.

Nichols JD, Kendall WL, Boomer GS. 2019. Accumulating evidence in ecology: Once is not enough. *Ecol Evol* 9:13991–14004.

Pattison-Williams JK, Xie L, Adamowicz WL, Pybus M, Hubbs A. 2020. An empirical analysis of hunter response to chronic wasting disease in Alberta. *Hum Dimens Wildl* 25:575–589.

Potapov A, Merrill E, Pybus M, Lewis MA. 2016. Chronic wasting disease: Transmission mechanisms and the possibility of harvest management. *PLoS One* 11: e0151039.

R Development Core Team. 2018. *A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Thompson WL, White GC, Gowen C. 1998. *Monitoring vertebrate populations*. Academic Press, San Diego, California, 365 pp.

US Geological Survey. 2020. *Distribution of chronic wasting disease in North America*. https://www.usgs.gov/media/images/distribution-chronic-wasting-disease-north-america-0. Accessed October 2020.

WAFWA (Western Association of Fish and Wildlife Agencies). 2017. *Recommendations for adaptive management of chronic wasting disease in the west*. WAFWA Wildlife Health Committee and Mule Deer Working Group, Edmonton, Alberta, Canada, and Fort Collins, Colorado, 20 pp.

Wild MA, Hobbs NT, Graham MS, Miller MW. 2011. The role of predation in disease control: A comparison of selective and nonselective removal on prion disease dynamics in deer. *J Wildl Dis* 47:78–93.

Williams ES, Young S. 1980. Chronic wasting disease of captive mule deer: A spongiform encephalopathy. *J Wildl Dis* 16:89–98.

Wolfe LL, Watry MK, Sirochman MA, Sirochman TM, Miller MW. 2018. Evaluation of a test and cull strategy for reducing chronic wasting disease prevalence in mule deer (*Odocoileus hemionus*). *J Wildl Dis* 54:511–519.

Zar JH. 2010. *Biostatistical analysis*. 5th Ed. Prentice Hall, Englewood Cliffs, New Jersey, 944 pp.

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