Evaluation of a wild white-tailed deer population management program for controlling chronic wasting disease in Illinois, 2003–2008

Nohra Mateus-Pinilla [a], Hsin-Yi Weng [b,*], Marilyn O. Ruiz [c], Paul Shelton [d], Jan Novakofski [e]

[a] Illinois Natural History Survey, University of Illinois Urbana-Champaign, 1816 S. Oak Street, Champaign, IL 61820, USA
[b] Department of Comparative Pathobiology, Purdue University, 625 Harrison Street, West Lafayette, IN 47907, USA
[c] Department of Pathobiology, University of Illinois at Urbana-Champaign, 2001 S. Lincoln Avenue, Urbana, IL 61801, USA
[d] Division of Wildlife Resources, Illinois Department of Natural Resources, One Natural Resources Way, Springfield, IL 62702, USA
[e] Department of Animal Sciences, University of Illinois at Urbana-Champaign, 205 Meat Science Laboratory, 1503 S. Maryland Drive, Urbana, IL 61801, USA

ARTICLE INFO

ABSTRACT

We evaluated population management programs for controlling chronic wasting disease (CWD) in wild white-tailed deer in Illinois between November 2002 and March 2008. The intervention consisted of measures of deer removal from three deer population control programs: Illinois Department of Natural Resources culling, deer population control permits and nuisance deer removal permits. We included in the analysis a total of 14,650 white-tailed deer CWD test results. These data also included location and demographic data collected from both deer harvested in the interventions as well as deer from hunter harvests and deer vehicle collisions. We quantified intervention pressures as the number of years of intervention, the total number of deer removed and the average number of deer removed per year. We accounted for temporal and spatial variations of intervention by using mixed logistic regression to model the association between intervention pressures and CWD prevalence change. The results showed that deer population management intervention as practiced in Illinois during the study period was negatively associated with CWD prevalence and the strength of association varied depending on age of deer and the measure of intervention pressure. The population management programs showed a more consistent association with reduced CWD prevalence in fawn and yearling white-tailed deer than in adult deer. Our results also suggested that frequent and continuing intervention events with at least moderate intensity of culling were needed to reduce CWD prevalence. A longer study period, however, is needed to make a more definite conclusion about the effectiveness of similar population management programs for controlling CWD in wild white-tailed deer.

© 2013 Elsevier B.V. Open access under CC BY-NC-ND license.

1. Introduction

Chronic wasting disease (CWD) is the only prion disease found in wild animals (Williams and Miller, 2002). It is a transmissible spongiform encephalopathy characterized by multiple neurological symptoms and is invariably fatal. CWD affects white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*)

* Corresponding author. Tel.: +1 765 494 0445; fax: +1 765 494 9830.
E-mail addresses: nohram@illinois.edu (N. Mateus-Pinilla),
weng9@purdue.eud (H.-Y. Weng), moruiz@illinois.edu (M.O. Ruiz),
Paul.Shelton@illinois.gov (P. Shelton), jnova@illinois.edu (J. Novakofski).

and moose (*Alces alces*) in North America (Williams and Young, 1980, 1982; Williams and Miller, 2002; Kahn et al., 2004; Kreeger et al., 2006; Argue et al., 2007; Baeten et al., 2007). Through 2008, CWD cases had been reported west to Utah and east as far as New York State (Salman, 2003; O'Rourke, 2005).

In Illinois, CWD was first identified from a suspect animal exhibiting clinical signs of disease in November 2002 (Illinois Department of Natural Resources, 2010), shortly after the discovery of CWD in Wisconsin deer harvested during the fall 2001 hunting season (Joly et al., 2003). In response, the Illinois Department of Natural Resources (IDNR) initiated a disease surveillance and deer population management intervention with the goal of controlling CWD. The central strategy of this intervention was to lower deer population densities by sharpshooting, particularly at winter aggregation sites in CWD infected and high risk areas. Population reduction to minimize disease transmission is a common component of infectious disease management strategies and some studies have suggested selective culling of infected individuals is useful to control CWD (Gross and Miller, 2001; Wasserberg et al., 2009; Potapov et al., 2012). In addition, a simulation study showed that the rate of CWD decay in the environment is proportional to the number of infected individuals, and that disease transmission is based on a frequency dependent approach where contact rates are independent of population density but dependent on social group sizes (Potapov et al., 2012). To that extent, the population management program in Illinois targeted deer social groups at wintering aggregation sites.

To our knowledge, only one study has been carried out to systematically evaluate deer population management for controlling CWD using empirical data (Conner et al., 2007). The main difficulties in conducting studies to evaluate CWD management include low disease prevalence, lengthy disease course, non-random allocation of intervention, time-varying exposure, and lack of individual level information for appropriate control of confounders. The goal of this study was to quantitatively assess the first five years of deer population management programs in Illinois for controlling CWD prevalence in wild white-tailed deer. Specifically, we used mixed logistic regression to model the association between this population management intervention and the CWD prevalence change. This approach allowed us to model the time-varying and multilevel nature of intervention assignment and to use statistical approaches to evaluate and adjust for confounding variables measured at both geographical and individual levels.

2. Materials and methods

2.1. Study area and sample

Our study area was determined by the minimum convex polygon of the maximum geographical extent (6708 km^2 and 2628 sections) where CWD cases were detected from November 2002 through March 2008 within seven counties in Illinois (Fig. 1). We included in the analysis a total of 14,650 white-tailed deer with CWD test results and with complete location and demographic data. We
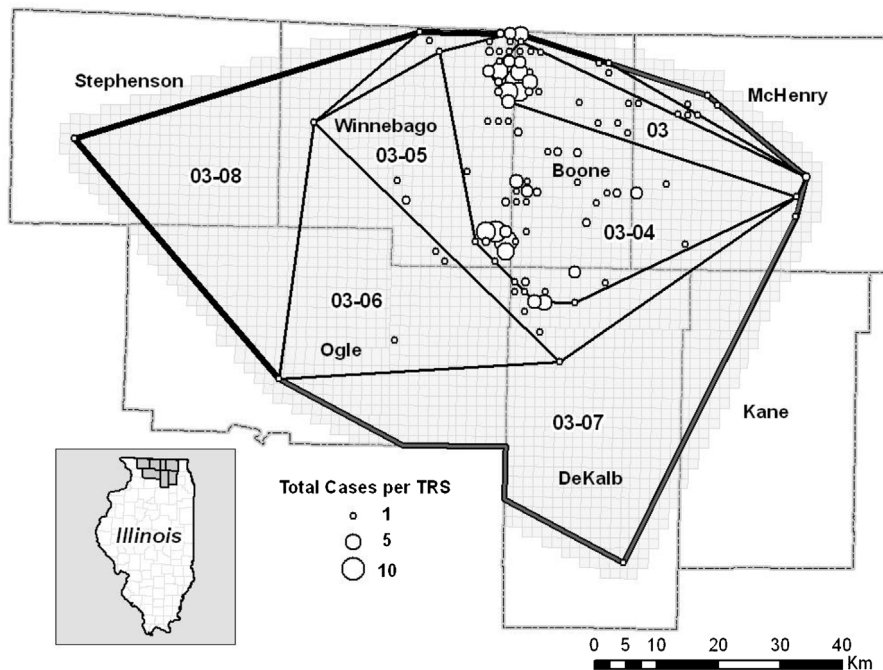

Fig. 1. Study area (6708 km^2 and 2628 sections) represented by the minimum convex polygon (MCP) around the accumulated cases of chronic wasting disease (CWD) detected during six time intervals occurring between harvest-years 2003 and 2008 in the seven-county CWD management area in northern Illinois. Location and number of positive cases are represented by section.

identified the location of individual deer records on a grid based on the Public Land Survey System "section" (~2.6 km^2) in which harvest occurred (Fig. 1). We used harvest date to assign a harvest-year to individual deer records. A harvest-year began July 1st and ended June 30th of the following calendar year named according to the ending calendar year. Each harvest-year included one fall hunter harvest and one winter culling-intervention period. A harvest-year roughly matches the life cycle of deer, which are born around May–June. Our study period therefore comprised the data collected between harvest-year 2003 and 2008.

2.2. Intervention and outcome variables

The study intervention consisted of three deer population control programs: Illinois Department of Natural Resources culling, deer population control permits and nuisance deer removal permits. We used the term "sharpshooting" to refer collectively to deer removed under those three programs. Sharpshooting location was assigned at the section level and varied each year according to the spatial distribution of CWD as portrayed by prior surveillance and deer density estimates. The decision to use section as the spatial unit for sharpshooting assignment was based on the available spatial data and financial and human resources to manage CWD in high disease transmission areas while minimizing stakeholder impact and maximizing opportunity to manage disease spread.

To best evaluate the intervention, three measures were used to quantify the pressure of sharpshooting applied to each section: (1) the number of years of sharpshooting, referred to as "frequency"; (2) the total number of deer removed by sharpshooting, referred to as "effort"; and (3) the average number of deer culled per year of sharpshooting (i.e., effort/frequency), referred to as "intensity". For analytic purpose, sharpshooting effort and intensity were categorized into five groups at 0 (no sharpshooting) and by their 75th, 90th and 95th percentiles.

Retropharyngeal lymph nodes and brain tissue (obex) from sampled deer were tested for CWD at the Illinois Department of Agriculture Animal Disease Laboratories in Galesburg and Centralia using immunohistochemistry. The study outcome variable was the binary test result of CWD (i.e., positive versus negative).

2.3. Study covariates

The study covariates included sex, age, and harvest source of deer, and environmental factors at the harvest locations. The selection of study covariates was based on our prior knowledge of their association with CWD (Miller and Wild, 2004; Farnsworth et al., 2005; Miller and Conner, 2005; Grear et al., 2006). Age and sex of deer were evaluated as potential effect modifiers or confounders in assessing the association between sharpshooting and CWD prevalence. All other covariates were examined as potential confounders.

Deer were categorized into fawn/yearling (6 to less than 24 months) or adult (24 months or older) classes using tooth eruption and wear (Severinghaus, 1949). Fawns less than six months of age were excluded from analysis because the long latency period for CWD greatly reduces the likelihood of detecting CWD in this age group. We categorized harvest source of deer into three groups for analysis: hunting, sharpshooting, and other. The hunter-harvested deer were obtained from firearm and archery seasons which took place from October through mid-January. The number of hunter-harvested deer tested for CWD depended on a predetermined monitoring quota and hunter voluntary submission of tissues. Therefore, these deer represented a subset of the total hunter-harvested deer at a given location. The deer obtained from deer vehicle collisions and from CWD suspect deer were classified into the category "other" in the analysis.

We measured environmental covariates related to deer density at the section level and assigned them to each deer record based on the section in which the deer was harvested. The size of contiguous forest (km^2) that overlapped a section was measured from forested land included in the Land Cover of Illinois 1999–2000 digital database (Illinois Department of Agriculture, 2001). The terrain variability was measured as the standard deviation of elevation from a Digital Elevation Model (United States Geological Survey, 2010). The soil texture-class most common in the section was selected from the United States Department of Agriculture (USDA) STATSGO maps (United States Department of Agriculture, 2010). Human population density was estimated from United States population census data block groups from 2000 (U.S. Census Bureau, 2010). The spatial data were processed using the ArcGIS 9.3 (ESRI, Redlands, CA) geographic information system (GIS). The environmental factors were categorized into binary variables as follows: (1) size of forest: ≤50 km^2 and >50 km^2, (2) terrain variability: ≤9.75 m, and >9.75 m, (3) soil texture: silt loam and other (which included gravelly loam, silty clay, and gravelly sandy loam), (4) human population density: ≤325 and >325 people per square mile.

2.4. Data analysis

We investigated temporal change in CWD prevalence during the study period between the harvest-years of 2003 and 2008 using chi-square test for trend. To assess the relationship between study covariates and CWD, we used logistic regression. While modeling the relationship between a particular covariate and CWD, the other covariates were evaluated for their confounding effects using a backward change-in-estimate procedure with a 10% change in odds ratio (OR) estimate as a cutoff value (Budtz-Jorgensen et al., 2007).

To model the association between the intervention and the change in CWD prevalence, we used mixed logistic regression. We included measures at both section and individual deer levels in our mixed logistic regression models. Because intervention assignments varied every year, we computed cumulative sharpshooting measures at the end of each harvest-year. For each time interval during the five-year study period, we modeled the association between the cumulative sharpshooting measures and the change in CWD prevalence with the assumption that the

intervention would affect CWD prevalence in the following year. For example, the intervention implemented during 2003–2005 would affect temporal change in CWD prevalence from 2003 to 2006, in which 2003 served as the baseline. We analyzed a total of 15 different time intervals during the study period from 2003 to 2008. Repeated measures and the multilevel nature of the data were accounted for in our mixed models. Robust estimation for testing fixed effects was used to handle potential violations of model assumption of covariance structures. Eq. (1) presents the key fixed effects in the mixed logistic regression.

$$\mathrm{logit}(P) = \beta_1 T + \beta_2 I + \beta_3 TI + \beta_m M + \beta_c C \qquad (1)$$

where β_1 is the regression coefficient for the time interval (T) under investigation. T is an index variable with a value of 0 indicating the initial harvest-year of a particular time interval and 1 indicating the end harvest-year of that interval. β_2 is the regression coefficient for cumulative intervention measure (I) during the time interval T. β_3 is the regression coefficient for the interaction term between T and I. β_m is the regression coefficient matrix for the covariate matrix of the 15 time intervals (M). β_c is the regression coefficient matrix for the selected covariate matrix (C).

Specifically, the mixed logistic regression models the association between the cumulative intervention pressure and the change in CWD prevalence odds while controlling for other covariates (i.e., C). The inclusion of the covariate matrix of M gave us a weighted average across all 15 investigated time intervals. The exponential of β_3 (i.e., the coefficient for the interaction term of T and I) was the parameter of interest, representing an adjusted OR, which quantified the strength and direction of the association between the cumulative intervention and the change in CWD prevalence odds. To build the mixed models, we first determined the effect modifications of age and sex of deer using a cutoff value of $P \leq 0.05$. Separate mixed models were constructed for significant effect modifiers. We then used the backward change-in-estimate procedure as previously described.

We defined $P \leq 0.05$ as statistical significance in this paper. SPSS 19 for Windows (SPSS Inc., Armonk, NY) was used to perform all data analyses.

3. Results

3.1. Distribution of intervention and CWD prevalence

Within the study area, about half (52%) of the harvested deer were from sections without intervention during harvest-year 2003–2008. The distributions of sharpshooting effort and intensity varied greatly across sections, ranging from 0 to 434 deer and from 0 to 108.5 deer per year of sharpshooting, respectively. Among sections with at least one sharpshooting event, the median sharpshooting frequency was three years, the median sharpshooting effort was 36 deer (interquartile range [IQR]: 15, 127) and the median sharpshooting intensity was 14.7 deer per year of sharpshooting (IQR: 7.0, 29.8). The overall CWD prevalence in the study area did not change between harvest-years 2003 and 2008 (P = 0.114; Table 1). The only significant trend in CWD prevalence observed during the study period was in fawn and yearling, ranging from 1.6% in 2004 to 0.6% in 2008 (P = 0.014; Table 1).

3.2. Study covariates and their relationship with CWD prevalence

We summarized the findings from the analysis of covariates in Table 2. All covariates showed a significant association with CWD except for human population density (P = 0.061; Table 2). Among them, harvest source and age of deer and terrain variability showed the strongest association with CWD prevalence. The hunter-harvested deer were less likely to have CWD than the deer taken from sharpshooting or other harvest sources. Adult deer were more likely to have CWD than fawns (OR = 4.5; 95% confidence interval (CI): 2.8, 7.4) and male deer were more likely to have CWD than female deer (OR = 1.8; 95% CI: 1.3, 2.4). Deer harvested at sections with high terrain variability (i.e., >9.75 m) were negatively associated with CWD while larger forest patches (>50 km^2) were positively associated with CWD risk.

3.3. Association between the intervention and the change in CWD prevalence

We identified age of deer as a significant effect modifier in all three measures of intervention pressure and

Table 1
Prevalence, expressed as percentage, of chronic wasting disease in the study area by harvest year and age and sex of deer. 95% confidence intervals of the estimated prevalence are in the parentheses.

Harvest year[a]	Overall	Fawn/yearling	Adult	Male	Female
2003	1.6 (0.9, 2.6)	1.1 (0.4, 2.7)	2.0 (0.9, 3.8)	1.4 (0.5, 3.2)	1.7 (0.8, 3.2)
2004	2.0 (1.5, 2.6)	1.6 (1.1, 2.4)	2.5 (1.7, 3.5)	2.3 (1.6, 3.4)	1.7 (1.2, 2.6)
2005	1.2 (0.9, 1.8)	0.6 (0.3, 1.3)	1.9 (1.3, 2.8)	1.2 (0.7, 2.0)	1.3 (0.8, 2.1)
2006	1.9 (1.4, 2.5)	1.2 (0.7, 1.9)	2.6 (1.9, 3.6)	2.0 (1.3, 2.9)	1.8 (1.2, 2.7)
2007	1.3 (1.0, 1.8)	0.7 (0.4, 1.2)	2.0 (1.4, 2.9)	1.5 (1.0, 2.3)	1.1 (0.7, 1.8)
2008	1.3 (1.0, 1.8)	0.6 (0.3, 1.1)	2.0 (1.4, 2.9)	1.4 (0.9, 2.2)	1.3 (0.8, 2.0)
Total n[b]	14,650	7588	6773	7898	6499
Trend test[c]	0.114	0.014	0.735	0.308	0.211

[a] Harvest year is defined as July 1 to the following June 30.
[b] Sum of the sample sizes across age groups and sex groups may not equal to the total due to missing data.
[c] P-value of the chi-square test for trend.

Table 2

Association between study covariates and prevalence of chronic wasting disease (CWD).

Covariates	n (%)	Number of CWD cases	OR (95% CI)[a]	P
Age[b]				<0.001
Fawn	2621 (18)	21	1	
Yearling	5039 (35)	51	2.1 (1.2, 3.6)	
Adult	6924 (47)	151	4.5 (2.8, 7.4)	
Sex[b]				<0.001
Female	8015 (55)	117	1	
Male	6608 (45)	109	1.8 (1.3, 2.4)	
Harvest source				<0.001
Hunting	8968 (61)	97	1	
Sharpshooting	5623 (38)	110	1.9 (1.4, 2.6)	
Other	59 (0.4)	19	34.3 (18.4, 64.1)	
Human population density				0.061
≤325	13,038 (89)	197	1	
>325	1612 (11)	29	0.7 (0.4, 1.0)	
Soil texture				0.030
Silt loam	11,866 (81)	196	1	
Other	2770 (19)	30	0.7 (0.4, 1.0)	
Terrain variability (m)				<0.001
Low ≤ 9.75	12,396 (85)	215	1	
High > 9.75	2254 (15)	11	0.3 (0.2, 0.5)	
Forest size (km²)				<0.001
≤50	8287 (57)	75	1	
>50	6363 (43)	151	2.7 (2.0, 3.5)	

[a] Odds ratio (OR) of CWD prevalence and corresponding 95% confidence interval (CI) are modeled using logistic regression and are adjusted for confounders. OR = 1 is the reference level for comparison.

[b] The total sample size is 14,650 deer, but samples used are 14,584 and 14,623 for age and sex related models to reflect missing data. Fawns: 6 to less than 12 months of age. Yearling: 12 to less than 24 months of age.

therefore built mixed logistic regression models for the two age groups separately (Table 3). We also identified sex of deer as a significant effect modifier but only in the intensity measure of sharpshooting ($P < 0.001$; Table 3). Hence, we investigated the association between the sharpshooting intensity and the change in CWD prevalence separately for age groups and sex of deer. We present the results of

Table 3

Confounder(s) identified in each of the mixed logistic regression used for modeling the effects of population management intervention (sharpshooting pressure) on chronic wasting disease. Different regression models for frequency and effort of sharpshooting were built by age of deer because of its effect modification. Intensity of sharpshooting is stratified by age and sex of deer because both of them are identified as effect modifiers.

Deer[a] (n)	Sharpshooting pressure[c]	Identified confounder
Fawn/yearling		
(7660)	Frequency	Harvest source
(7660)	Effort	Harvest source
(7660)	Intensity	Harvest source
Adult		
(6924)	Frequency	Harvest source
(6913)[b]	Effort	Sex of deer, harvest source
(6913)[b]	Intensity	Sex of deer
Female		
(8015)	Intensity	None
Male		
(6588)	Intensity	Age of deer

[a] The sample size varies to reflect missing values in the model.

[b] 6924 minus 11 deer without sex information.

[c] Sharpshooting pressure is quantified as sharpshooting frequency (i.e., number of years of sharpshooting), effort (i.e., total number deer removed by sharpshooting), and intensity (i.e., average number of deer culled per year of sharpshooting).
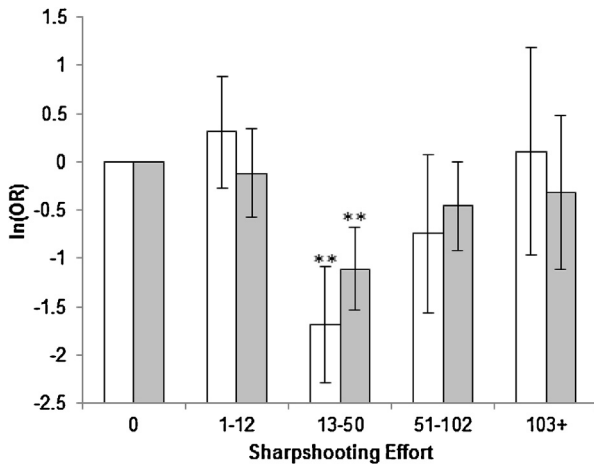
covariate selections for each of the mixed logistic regression models in Table 3.

When measuring intervention pressure by frequency, we observed a significant negative association with the change in CWD prevalence in fawns and yearlings when intervention was applied every year during the 5-year period from 2003 to 2007 ($P < 0.001$). When measuring intervention by effort we found a non-linear association with CWD prevalence with the removal of 13–50 deer during the 5-year intervention period showing the strongest effect on reducing CWD prevalence (Fig. 2). Removal of 13–50 deer during the 5-year intervention period reduced the CWD prevalence by 0.33-fold (95% CI: 0.14, 0.76) in fawns and yearlings ($P = 0.009$) and by 0.19-fold (95% CI: 0.06, 0.60) in adults ($P = 0.005$) compared to no sharpshooting. We also observed a non-linear relationship between intensity and CWD prevalence in all four age and sex strata, although the observed associations were only significant in the sex strata (Figs. 3 and 4). Regardless of statistical significance, we observed a stronger and more consistent association between intensity and CWD prevalence reduction in fawn and yearling deer than in adult deer (Fig. 3). A low intensity of less than or equal to eight deer per year of sharpshooting and a moderate intensity of 28.1–59.0 deer per year of sharpshooting showed significant negative association with CWD prevalence change in males with the OR of 0.36 (95% CI: 0.14, 0.92; $P = 0.033$) and 0.37 (95% CI: 0.14, 0.94; $P = 0.037$), respectively, compared to no sharpshooting (Fig. 4). Similarly, a moderate intensity showed significant negative association with the change in CWD prevalence in female deer compared to no sharpshooting (Fig. 4). An intensity of 8.1–28.0 deer per year of sharpshooting reduced CWD prevalence by 0.36-fold (95% CI: 0.15, 0.84; $P = 0.019$) and an intensity of 28.1–59.0

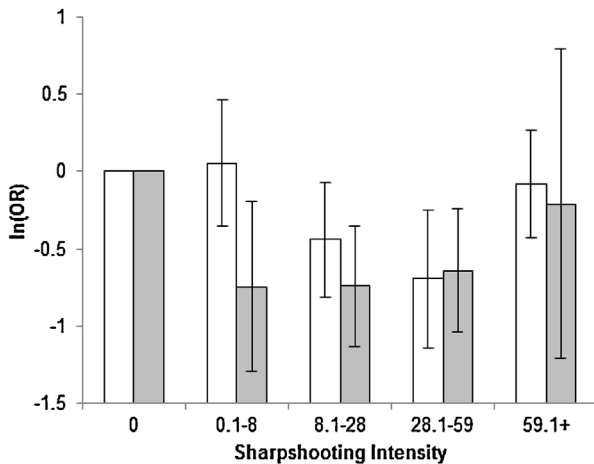**Fig. 2.** Association between different number of deer removed by population management intervention (sharpshooting effort) and change in chronic wasting disease expressed as natural logarithmic transformed odds ratio (ln(OR)). Sections with no sharpshooting (i.e., sharpshooting effort of 0) were used as the reference group for ln(OR) computations. Error bars are standard errors of ln(OR). Empty columns present adult deer and gray columns present fawn and yearling deer. **Indicates *P* < 0.01.

Fig. 4. Association between different number of deer culled per year of population management intervention (sharpshooting intensity) and change in chronic wasting disease expressed as natural logarithmic transformed odds ratio (ln(OR)). Sections with no sharpshooting (i.e., sharpshooting intensity of 0) were used as the reference group for ln(OR) computations. Error bars are standard errors of ln(OR). Empty columns present female deer and gray columns present male deer. *Indicates *P* < 0.05.

Fig. 3. Association between different number of deer culled per year of population management intervention (sharpshooting intensity) and change in chronic wasting disease expressed as natural logarithmic transformed odds ratio (ln(OR)). Sections with no sharpshooting (i.e., sharpshooting intensity of 0) were used as the reference group for ln(OR) computations. Error bars are standard errors of ln(OR). Empty columns present adult deer and gray columns present fawn and yearling deer.

deer per year of sharpshooting reduced CWD prevalence by 0.40-fold (95% CI: 0.18, 0.88; *P* = 0.022) compared to no sharpshooting in females (Fig. 4).

4. Discussion

In this study, we evaluated the population management programs implemented from harvest-year 2003 to 2007 in Illinois for controlling CWD in wild white-tailed deer over a 6-year period (harvest-year 2003–2008). Foreseeing the importance of public and societal acceptance of deer population control programs to the success of
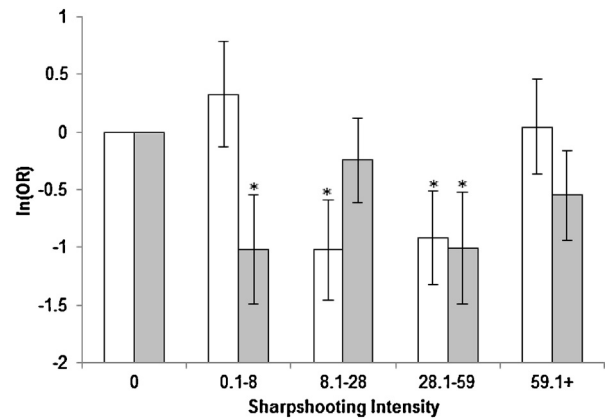
disease management efforts (de Lisle et al., 2002; O'Brien et al., 2006; Carstensen et al., 2011), Illinois minimized the negative human impact and public opposition by supporting liberalized hunting regulations (i.e., additional season days and increased permit quotas where possible) and treating the deer population management program as a long term effort to control CWD rather than an aggressive CWD eradication program as implemented in Wisconsin in early 2000s, which turned out to be an unsuccessful CWD management strategy (Heberlein, 2004; Holsman et al., 2010; VerCauteren and Hygnstrom, 2011).

Culling has been used to control different diseases in wildlife populations, however not all diseases respond similarly to this method. For example, culling was identified as an efficient way for controlling classical swine fever in wild pigs (Cowled et al., 2012) but showed varied results in controlling bovine tuberculosis in free-ranging wildlife in different countries (O'Brien et al., 2011) and was not effective for controlling the Aujeszky's disease in wild boars (Boadella et al., 2012). The different responses appeared to be associated with continual viral shedding and proportion of hosts excreting the virus as well as public acceptance of the control program.

The finding that the association between intervention and the change in CWD prevalence differed between fawn/yearling and adult deer was worth noting. Recognizing that CWD diagnostic results used in this study were not stratified by lymphatic or neurological test results to differentiate early compared to advanced infection, it is reasonable to speculate that CWD cases in young deer reflect incident cases. In this study, we observed a more consistent association with reduced CWD prevalence in young deer implying that intervention could reduce the number of new infections and providing an important benchmark for future management. This finding also agreed with our observation of a significant (*P* = 0.014)

declining trend in CWD prevalence in fawn and yearling deer during the study period.

We used three sharpshooting measures, frequency, effort and intensity, to quantify the pressure of intervention. The intention of using these different measures was to fully elucidate the optimal management strategy. This approach allowed us to address the question: "Is it sufficient to have a particular number of deer removed or is it necessary to have a particular number of years of sharpshooting or is it necessary to remove an average number of deer per year of intervention to impact CWD prevalence in high risk areas?" We observed a significant reduction in CWD prevalence in fawns and yearlings in the sections that had sharpshooting implemented every year during the 6-year study period compared to the sections with no sharpshooting. However, due to the small number of cases in this highest sharpshooting frequency group, we were not able to make a precise estimate. In contrast to frequency, a non-linear relationship was observed between effort, intensity and CWD prevalence. Those results indicated that removing only a moderate number of deer had a stronger association with reduced CWD prevalence than removing a large number of deer. However, the overlapping of 95% CIs (Fig. 2) indicates that the relationships between these categories and the change in CWD prevalence are not significantly different from each other. Combining the findings from all three sharpshooting measures, our data suggest a continuing sharpshooting intervention that removes at least a moderate number of deer is necessary to control CWD in free-ranging deer. A larger sample size accumulated over a longer time period is needed to make a more definite recommendation on the optimal deer population control strategy for CWD management. Furthermore, the maximum effort and intensity are limited by the deer population size in an area, with culling of larger numbers of deer only possible in more densely populated areas. These high density areas may require more time to bring about significant population reductions, potentially forestalling changes in CWD prevalence. Although we controlled for the confounding effects of the environmental measures that were known to be related to deer population density in our statistical models, the estimated association between sharpshooting and change in CWD prevalence may still be biased due to residual confounding.

Several limitations of our surveillance sampling must be considered when assessing the association between the intervention and the change in CWD prevalence. First, the selection of sections for intervention was dependent on CWD prevalence. These sections were expected by design to have a greater than overall prevalence of CWD. Second, passive and active surveillance may not provide equally representative samples of the population each year. These sources of bias must be considered in study design and/or data analysis while evaluating CWD management programs. Conner et al. (2007) took into account these potential sources of bias by matching treatment with non-treatment (control) areas to make them similar with respect to landscape features. The assumption was that paired treatment-control areas were comparable with respect to the distribution of all covariates associated with CWD within the defined geographic group.

Our approach, however, had many distinguishing features from the Conner et al. (2007) approach. First, the distinctly different environments found in their study are not typical of the Illinois study region and therefore limited adoption of their analytical method. Second, our use of mixed logistic regression allowed us to evaluate study covariates quantitatively, at both individual deer and section levels, for their roles as effect modifiers (age and sex of deer only) or confounders. Third, we used three different measures to quantify the pressure of intervention and took into account the time-varying and multilevel nature of intervention assignment in data analysis. Instead of investigating the association between sharpshooting and change in CWD prevalence for a fixed time interval, our approach allowed us to generate a weighted average across different time frames. While Conner et al. concluded from their study that benefits of population management program were not evident, our study showed that the association between the deer population management intervention and the change in CWD prevalence was present but was not uniform. The strength of association depended on sharpshooting pressure and age of deer.

In this study, we analyzed the data collected from the first six years of intervention in Illinois, which was a relatively short period considering the chronic nature of CWD. This limited study period also confined our study findings to a limited range of sharpshooting measures. In addition, public acceptance is the key to the success of such a free-ranging deer population management program. Unfortunately, Illinois faces significant challenges associated with stakeholder and societal acceptance. Nevertheless, management of CWD will require a continual commitment to intervention and the integrative collaboration of multiple stakeholders. The findings from our study warrant additional studies evaluating similar deer population management programs on controlling CWD in wild white-tailed deer.

5. Conclusion

In this study, we evaluated the wild white-tailed deer population management intervention implemented in Illinois for controlling CWD between 2003 and 2008. The findings suggest that frequent and continuing sharpshooting events are needed to reduce CWD prevalence. A longer study period, however, is needed to make a more definite recommendation on the optimal white-tailed deer population management strategy for controlling CWD.

Conflict of interest

None of the authors of this paper have any financial or personal relationship with other persons or organizations that could inappropriately influence or bias the content of this paper.

References

Argue, C.K., Ribble, C., Lees, V.W., McLane, J., Balachandran, A., 2007. Epidemiology of an outbreak of chronic wasting disease on elk farms in Saskatchewan. Can. Vet. J. 48, 1241–1248.

Baeten, L.A., Powers, B.E., Jewell, J.E., Spraker, T.R., Miller, M.W., 2007. A natural case of chronic wasting disease in a free-ranging moose (*Alces alces* shirasi). J. Wildl. Dis. 43, 309–314.

Boadella, M., Vincente, J., Ruiz-Fons, F., de la Fuente, J., Gortázar, C., 2012. Effects of culling Eurasian wild boar on the prevalence of *Mycobacterium bovis* and Aujeszky's disease virus. Prev. Vet. Med. 107, 214–221.

Budtz-Jorgensen, E., Keiding, N., Grandjean, P., Weihe, P., 2007. Confounder selection in environmental epidemiology: assessment of health effects of prenatal mercury exposure. Ann. Epidemiol. 17, 27–35.

Carstensen, M., O'Brien, D.J., Schmitt, S.M., 2011. Public acceptance as a determinant of management strategies for bovine tuberculosis in free-randing U.S. wildlife. Vet. Microbiol. 151, 200–204.

Conner, M.M., Miller, M.W., Ebinger, M.R., Burnham, K.P., 2007. A meta-BACI approach for evaluating management intervention on chronic wasting disease in mule deer. Ecol. Appl. 17, 140–153.

Cowled, B.D., Garner, M.G., Negus, K., Ward, M.P., 2012. Controlling disease outbreaks in wildlife using limited culling: modelling classical swine fever incursions in wild pigs in Australia. Vet. Res. 43, 3.

de Lisle, G.W., Bengis, R.G., Schmitt, S.M., O'Brien, D.J., 2002. Tuberculosis in free-raning wildlife: detection, diagnosis and management. Rev. Sci. Technol. 21, 317–334.

Farnsworth, M.L., Wolfe, L.L., Hobbs, N.T., Burnham, K.P., Williams, E.S., Theobald, D.M., Conner, M.M., Miller, M.W., 2005. Human land use influences chronic wasting disease prevalence in mule deer. Ecol. Appl. 15, 119–126.

Grear, D.A., Samuel, M.D., Langenberg, J.A., Keane, D., 2006. Demographic patterns and harvest vulnerability of chronic wasting disease infected white-tailed deer in Wisconsin. J. Wildl. Manage. 70, 546–553.

Gross, J.E., Miller, M.W., 2001. Chronic wasting disease in mule deer: disease dynamics and control. J. Wildl. Manage. 65, 205–215.

Heberlein, T.A., 2004. "Fire in the Sistine Chapel": how Wisconsin responded to chronic wasting disease. Hum. Dimens. Wildl. 9, 165–179.

Holsman, R.H., Petchenik, J., Cooney, E.E., 2010. CWD after "the Fire": six reasons why hunters resisted Wisconsin's eradication effort. Hum. Dimens. Wildl. 15, 180–193.

Illinois Department of Agriculture, 2001. Land Cover of Illinois 1999–2000. http://www.agr.state.il.us/gis/landcover99-00.html (accessed 20.11.10).

Illinois Department of Natural Resources (IDNR), 2010. CWD Information. http://dnr.state.il.us/cwd/ (accessed 23.12.10).

Joly, D.O., Ribic, C.A., Langenberg, J.A., Beheler, K., Batha, C.A., Dhuey, B.J., Rolley, R.E., Bartelt, G., Van Deelen, T.R., Samuel, M.D., 2003. Chronic wasting disease in free-ranging Wisconsin white-tailed deer. Emerg. Infect. Dis. 9, 599–601.

Kahn, S., Dube, C., Bates, L., Balachandran, A., 2004. Chronic wasting disease in Canada: part 1. Can. Vet. J. 45, 397–404.

Kreeger, T.J., Montgomery, D.L., Jewell, J.E., Schultz, W., Williams, E.S., 2006. Oral transmission of chronic wasting disease in captive Shira's moose. J. Wildl. Dis. 42, 640–645.

Miller, M.W., Conner, M.M., 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, M.W., Wild, M.A., 2004. Epidemiology of chronic wasting disease in captive white-tailed and mule deer. J. Wildl. Dis. 40, 320–327.

O'Brien, D.J., Schmitt, S.M., Fitzgerald, S.D., Berry, D.E., Hickling, G.J., 2006. Management the wildlife reservoir of *Mycobacterium bovis*: the Michigan, USA, experience. Vet. Microbiol. 112, 313–323.

O'Brien, D.J., Schmitt, S.M., Rudolph, B.A., Nugent, G., 2011. Recent advances in the management of bovine tuberculosis in free-ranging wildlife. Vet. Microbiol. 151, 23–33.

O'Rourke, K., 2005. CWD found in New York. J. Am. Vet. Med. Assoc. 226, 1633.

Potapov, A., Merrill, E., Lewis, M.A., 2012. Wildlife disease elimination and density dependence. Proc. R. Soc. B 279, 3139–3145.

Salman, M.D., 2003. Chronic wasting disease in deer and elk: scientific facts and findings. J. Vet. Med. Sci. 65, 761–768.

Severinghaus, C.W., 1949. Tooth development and wear as criteria of age in white-tailed deer. J. Wildl. Manage. 13, 195–216.

United States Department of Agriculture (USDA), 2010. Natural Resources Conservation Service. U.S. General Soil Map (STATSGO2) http://soils.usda.gov/survey/geography/statsgo/ (accessed 20.11.10).

United States Geological Survey (USGS)D 2010, http://seamless.usgs.gov/index.php (accessed 20.11.10).

U.S. Census Bureau, 2010. http://www.census.gov (accessed 20.11.10).

VerCauteren, K.C., Hygnstrom, S.E., 2011. Managing white-tailed deer: Midwest North America. In: Biology and Management of White-tailed Deer, Boca Raton, FL, pp. 501–535.

Wasserberg, G., Osnas, E.E., Rolley, R.E., Samuel, M.D., 2009. Host culling as an adaptive management tool for chronic wasting disease in white-tailed deer: a modelling study. J. Appl. Ecol. 46, 457–466.

Williams, E.S., Miller, M.W., 2002. Chronic wasting disease in deer and elk in North America. Rev. Sci. Tech. 21, 305–316.

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

Williams, E.S., Young, S., 1982. Spongiform encephalopathy of Rocky Mountain elk. J. Wildl. Dis. 18, 465–471.