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DETECTION OF BIAS IN HARVEST-BASED ESTIMATES OF CHRONIC WASTING DISEASE PREVALENCE IN MULE DEER

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ABSTRACT: Diseased animals may exhibit behavioral shifts that increase or decrease their probability of being randomly sampled. In harvest-based sampling approaches, animal movements, changes in habitat utilization, changes in breeding behaviors during harvest periods, or differential susceptibility to harvest via behaviors like hiding or decreased sensitivity to stimuli may result in a non-random sample that biases prevalence estimates. We present a method that can be used to determine whether bias exists in prevalence estimates from harvest samples. Using data from harvested mule deer (*Odocoileus hemionus*) sampled in northcentral Colorado (USA) during fall hunting seasons 1996–98 and Akaike's information criterion (AIC) model selection, we detected within-yr trends indicating potential bias in harvest-based prevalence estimates for chronic wasting disease (CWD). The proportion of CWD-positive deer harvested slightly increased through time within a yr. We speculate that differential susceptibility to harvest or breeding season movements may explain the positive trend in proportion of CWD-positive deer harvested during fall hunting seasons. Detection of bias may provide information about temporal patterns of a disease, suggest biological hypotheses that could further understanding of a disease, or provide wildlife managers with information about when diseased animals are more or less likely to be harvested. Although AIC model selection can be useful for detecting bias in data, it has limited utility in determining underlying causes of bias. In cases where bias is detected in data using such model selection methods, then design-based methods (i.e., experimental manipulation) may be necessary to assign causality.

Key words: Chronic wasting disease, harvest sampling, modeling, mule deer, *Odocoileus hemionus,* prevalence, sample bias.

INTRODUCTION

Sampling is a fundamental component of many wildlife disease investigations. Time and budget constraints frequently prevent complete population census, and consequently disease prevalence is routinely estimated from a sample. State and federal agencies responsible for monitoring wildlife health often rely on samples from individuals harvested by hunters to estimate disease prevalence (e.g., Schmitt et al., 1997; Gallivan et al., 1998; Miller et al., 2000). This approach, while cost effective, usually assumes that all individuals are harvested at random. Sampling bias may occur for a variety of reasons, including differential susceptibility to harvest for infected animals compared to uninfected animals (Courchamp et al., 2000), seasonal changes in habitat use, seasonal changes in animal distribution due to migration movements, or behavioral changes related to the breeding season. Harvest samples are often collected over a long enough time period to evaluate bias in prevalence estimates, but such evaluations are rarely undertaken.

Chronic wasting disease (CWD), a transmissible spongiform encephalopathy, occurs naturally in some free-ranging mule deer (*Odocoileus hemionus*) populations in Colorado and Wyoming, USA (Miller et al., 2000). Clinical signs of CWD include initially subtle abnormal behavior that gets progressively worse, as well as desensitization to external stimuli and poor body condition in later stages of disease (Williams and Young, 1992). It follows that CWD-infected mule deer could have a higher or lower probability of harvest compared to uninfected deer, depending on disease state. For example, if infected deer appear healthy but wander aimlessly or are

TABLE 1. Hunting seasons and data sampling periods for chronic wasting disease surveys in game management units (9, 19, 191, and 20) in Larimer County, Colorado (Miller et al., 2000).

Year(i)	Archery/muzzleloading 1st sampling period in year(i)	Rifle 1 2nd sampling period in year(i)	Rifle 2 3rd sampling period in year(i)	Rifle 3 4th sampling period in year(i)
1996	9 Sep–1 Oct	12 Oct–18 Oct	19 Oct–1 Nov	2 Nov–30 Nov
1997	15 Aug–1 Oct	11 Oct–17 Oct	18 Oct–31 Oct	1 Nov–30 Nov
1998	1 Sep–1 Oct	10 Oct–16 Oct	17 Oct–30 Oct	31 Oct–30 Nov

less sensitive to external stimuli, then they may be oblivious to hunters and harvested more easily than healthy deer, resulting in a biased overestimate of CWD prevalence. Conversely, deer in poor body condition could be lethargic and remain in hiding or could be avoided by hunters, resulting in an underestimate of CWD prevalence. These biases could be manifested as an increase or decrease in the proportion of CWD-positive deer harvested over time within a sampling period, resulting in over- or underestimation of prevalence.

Here we describe a model-selection strategy to detect changes in CWD-prevalence estimates through time that may indicate bias. We used data from harvested mule deer sampled in northcentral Colorado during fall hunting seasons 1996-98 and Akaike's information criterion corrected for small sample sizes (AICc) (Akaike, 1973; Burnham and Anderson, 1998) to detect changes in CWD-prevalence estimates through time that may indicate bias. Information criteria model selection balances the trade-off between bias and precision of an estimator (Burnham and Anderson, 1998) and has numerous advantages over traditional methods of model selection used in regression (McQuarrie and Tsai, 1998). AICc is one of the most widely used information-based model selection procedures (Hurvich and Tsai, 1989). This criterion is based on maximum likelihood theory and is related to likelihood ratio testing (Buckland et al., 1997; Burnham and Anderson, 1998). Using AICc expands likelihood ratio tests, which compare only two models at a time, by allowing comparison and selection of a best approximating model from a suite of models; moreover AICc allows for comparison of non-nested models. Under this approach, biologically reasonable relationships between confounding variables, such as age and sex, and independent variables, such as treatment or sampling method, can be combined in a priori hypotheses represented by models. Models incorporating a time trend, with other necessary independent variables, can be used to test for bias in prevalence estimates.

MATERIALS AND METHODS

The Colorado Division of Wildlife (CDOW) has been using harvest-based surveys to estimate CWD prevalence since 1990 (Miller et al, 2000). Although a large number of game management units (GMUs) have been surveyed, only a few areas were sampled consistently and intensely from year to year. GMUs 9, 19, 191, and 20 were the most intensively sampled during 1996–98 (Miller et al., 2000). We use these 4 GMUs in our analyses because sample sizes were large, CWD prevalence was relatively high, and sampling efforts were intensive. There were no fawns in our sample; thus all analyses pertain to mule deer >1-yr-old.

Harvested deer were sampled during four fall hunting seasons within each year during 1996-98 (Table 1). Portions of the medulla oblongata were collected from 1370 harvested mule deer from GMUs 9, 19, 191, and 20 and tested for CWD (Table 2) using methods described by Miller et al. (2000). Briefly, formalin-fixed medulla oblongatas, sectioned at the obex, were examined for PrP^{res} accumulations by IHC (Miller et al., 1993; Sparker et al., 1997; O'Rourke et al., 1998) and lesions (Williams and Young, 1993; Spraker et al., 1997) consistent with CWD infection. All IHC-positives and most -negatives were evaluated independently by histopathology. Pathologists were blinded to samples' precise GMU origins. Samples showing positive IHC reactions, with

TABLE 2. Harvest sample sizes and number of deer testing positive for chronic wasting disease during fall hunting seasons (sampling periods) in game management units '9, 19, 191, and 20'; Larimer County, Colorado, 1996–98.

	Number positive for CWD/ Number tested for CWD; all years summed			
Sex	1st sampling period	2nd sampling period	3rd sampling period	4th sampling period
Male	1/34	9/271	30/464	19/293
Female	3/74	3/71	4/80	5/83

or without spongiform encephalopathy, were classified as CWD-positive.

Because these data were collected through time during four hunting seasons within each year, prevalence estimates could be evaluated for time trends that would suggest possible bias. We developed five logistic regression models that expressed our hypotheses about bias in CWD prevalence and then used AICc to pick the best approximating model for the field data.

Whether an animal tested positive or negative for CWD was a binary response variable. Logistic regression is commonly used to examine the relationship between a dependent binomial variable, such as a positive or negative CWD test, and independent continuous or categorical variables (Agresti, 1996). The kernel of the log-likelihood of this regression model is:

$$\sum_{S=1}^{4} [n_p \log(\hat{p}_S) + n_n \log(1 - \hat{p}_S)],$$

where S is the fall hunting season, with 1 being the first season, 2 being the second season etc. For each fall hunting season, n_p is the number of deer testing positive, n_n is the number of deer testing negative, and $\hat{p}_s$ estimated proportion of deer testing positive in the population (estimated from the sample). The logistic or logit transformation is given by:

$$\text{logit}(p_S) = \log\left(\frac{p_S}{1 - p_S}\right) = \beta_0 + \beta_1(S),$$

which constrains the proportion of deer harvested with CWD per season to be $0 \leq p_s \leq 1$. β_0 is the intercept and β_1 is the slope.

We used an intercept to model our first hypothesis, that our harvest sample provided an unbiased estimate of CWD prevalence. Here, the proportion of CWD-positive deer harvested represents the proportion of deer in the population having CWD, which remains constant from season to season:

$$\text{logit}(p) = \beta_0,$$

where p was the mean proportion of CWD-positive deer harvested for all four hunting seasons. To model our second hypothesis, that there may be a bias in estimates of CWD prevalence, we used a time trend model. Here, the estimated proportion of CWD-positive deer increases or decreases through time:

$$\text{logit}(p_s) = \beta_0 + \beta_1 (S),$$

where p_s was the proportion of CWD-positive deer harvested for hunting season S.

We included two additional models to make sure that prevalence estimates were not affected by hunting method (archery/muzzleloading versus rifle). Thus, in addition to the first two models (Table 3, Model 1, 2), we similarly developed two models incorporating a possible hunting method effect (Table 3, Model 3, 4). Finally, we developed one model to account for unexplained changes in proportion of CWD-positive deer harvested (Table 3, Model 5). Model 5 allows the proportion of CWD-positive deer to be different for each season, and often is used for time series analyses. If model 5 is selected, we conclude that there were no potential biases in prevalence estimates, but high variation. The biological hypotheses tested by respective models were: (1) the harvest sample was not biased: that is, it contained the same proportion of CWD-positive deer as exists in the population; (2) the harvest sample contained a bias; that is, the proportion of CWD-positive deer harvested changed through time, regardless of hunting method; (3) the harvest sample contained a bias only during rifle hunting seasons; that is, the proportion of CWD-positive deer harvested changed through time for rifle hunting; (4) deer with CWD were differentially susceptible to method of harvest (archery/muzzleloading versus rifle); and (5) there was unexplained high variation in the susceptibility of CWD-positive deer harvested from season to season.

We then used AICc to select which of these five models best fit the data. AICc was defined as:

$$\text{AICc} = -2 \ln(l) + 2K + \frac{2K(K + 1)}{n - K + 1},$$

where in (l) is the natural logarithm of the likelihood function evaluated at the maximum likelihood estimates for a given model, K is the number of estimable parameters from that model, and n is sample size. Models were ranked and compared using ΔAICc (Leberton et al., 1992, Burnham and Anderson, 1998). For the suite of models being compared, Δ-AICc was computed for each model as:

TABLE 3. Description and structure of *a priori* models relating effects of hunting seasons on proportion of deer infected with chronic wasting disease.

Model	Hypothesis description	Model structure[a]
1	Intercept model: the proportion of deer harvested with CWD was constant from season to season.	β_0
2	Trend model: the proportion of deer harvested with CWD increases or decreases over the 4 hunting seasons.	$\beta_0 + \beta_1(S)$
3	Modified trend model: the proportion of deer harvested with CWD increases or decreases only over the 3 rifle hunting seasons.	$\beta_0 + \beta_1(R)$
4	Hunting method model: the proportion of deer harvested with CWD was different by hunting method, archer/muzzleloading versus rifle hunting.	$\beta_0 + \beta_1(M)$
5	Time model: the proportion of deer harvested with CWD varies without a trend from season to season.	$\beta_0 + \beta_1(R1) + \beta_2(R2) + \beta_3(R3)$

[a] S represents all hunting seasons (archery/muzzleloading, rifle 1, rifle 2, and rifle 3), R represents rifle hunting seasons, M represents hunting method (archery/muzzleloading or rifle), and R1, R2, and R3 represent rifle 1, rifle 2, and rifle 3 respectively. The dependent variable, proportion of deer infected with CWD by season (p_s) was in logit scale.

$$\Delta AICc_i = AICc_i - AICc_{min},$$

where $AICc_i$ was the AICc value for the ith model and $AICc_{min}$ was the minimum AICc among the suite of models being compared. Essentially, $\Delta AICc_i$ is an estimate of the distance between the best approximating model and all other models evaluated, with the best model having the lowest AICc. Only models $\Delta AICc \leq 3$ were considered good candidates for explaining patterns in the field data (Burnham and Anderson, 1998); we considered models with $\Delta AICc > 5$ as having little support for explaining patterns in field data and models with $\Delta AICc > 10$ as having no support (Burnham and Anderson, 1998). Parameter estimates and AICc values were calculated using PROC GENMOD (SAS Institute, 1993).

Although we could not include age in our models because age data were only collected during 1998, we used these data to evaluate whether the age distribution of harvested deer changed during the sampling period. Deer were recorded as being 1-, 2-, or ≥3-yr-old. Specifically, for 1998 data, we used a chi-square test of independence to evaluate whether age was independent of sampling period. We also estimated proportion of older (≥3-yr-old) deer harvested per season.

RESULTS

Because males were harvested at much greater rates than females, and because the estimated sex ratio in GMUs studied was about 30 males: 100 females, we analyzed data separately for each sex. For our field data set, prevalence was not different between yr in sampled GMUs (Chi-Square $df = 1$, $n = 1{,}371$, $P = 0.642$). Consequently, we combined data across yr in our analyses. For both sexes, the best model was a 3-rifle season trend model (Table 4, Model 3), which was $\Delta AICc > 9$ than the next best model. Thus, we considered Model 3 as the only good model for explaining patterns in the field data. Additionally, we tested whether trends varied between yr additively or multiplicatively compared to the single trend model (no yr effect) using likelihood ratio tests. Neither the additive model nor the multiplicative models were significantly better than the single trend model for male data (χ^2 $df = 1$, $P = 0.322$ and $df = 2$, $P = 0.284$ respectively) or for female data (χ^2 $df = 1$, $P = 0.167$ and $df = 2$, $P = 0.278$ respectively). Thus, a single trend represented prevalence for all three yr data were collected (Fig. 1). For both sexes, CWD prevalence increased through the rifle seasons as indicated by the positive slope (Fig. 1).

To compare AICc model selection to more traditional methods, we also performed a likelihood ratio test between the intercept and 3-season trend model. From

TABLE 4. Ranking of *a priori* hypothesized models relating effects of hunting seasons on proportion of deer infected with chronic wasting disease ranked by Akaike's information criterion corrected for small sample sizes in game management units '9, 19, 191, and 20'; Larimer County, Colorado, 1996–98.

Model structure and description[a]	Model number	AICc	ΔAICc[b]
Males:			
$\beta_0 + \beta_1$(R): 3-rifle season trend	3	447.71	0.00
$\beta_0 + \beta_1$(S): 4-season trend	2	456.73	9.03
β_0: intercept	1	457.84	10.14
$\beta_0 + \beta_1$(R1) + β_2(R2) + β_3(R3): random variation between seasons	5	459.22	11.51
$\beta_0 + \beta_1$(M): archery/muzzleloading versus rifle hunting	4	459.31	11.60
Females:			
$\beta_0 + \beta_1$(R): 3-rifle season trend	3	98.44	0.00
β_0: intercept	1	121.93	23.49
$\beta_0 + \beta_1$(S): 4-season trend	2	123.58	25.13
$\beta_0 + \beta_1$(M): archery/muzzleloading versus rifle hunting	4	123.81	25.37
$\beta_0 + \beta_1$(R1) + β_2(R2) + β_3(R3): Random variation between seasons	5	127.65	29.20

[a] S represents all hunting seasons (archery/muzzleloading, rifle 1, rifle 2, and rifle 3), R represents rifle hunting seasons, M represents hunting method (archery/muzzleloading or rifle), and R1, R2, and R3 represent rifle 1, rifle 2, and rifle 3 respectively. The dependent variable, proportion of deer infected with CWD by season (P_s) was in logit scale.

[b] Models with ΔAICc ≤3 were considered good candidates for explaining patterns in field data, models with ΔAICc >5 had little support, and models with ΔAICc >10 had essentially no support.

the intercept model, the mean prevalence for all seasons was 5.4% (95% CI = 4.2–6.6%) for males. The 3-season trend model was a better approximating model than the intercept model for male data (χ^2 df = 1, $P < 0.001$) and female data (χ^2 df = 1, $P < 0.001$), in agreement with AICc model selection results.

Only two female deer were sampled in the study area in 1998 so only male deer were used in age analyses. For 1998, the age of a harvested male deer was independent of the season of harvest (χ^2 df = 4, n = 433, P = 0.420). Specifically, the proportion of older (≥3-yr-old) male deer harvested did not significantly differ between sampling periods as all confidence intervals overlapped. The proportion of older male deer harvested was 0.45 (95% CI = 0.35–0.55) in the 2nd sampling period, 0.55 (95% CI = 0.48–0.62) in the 3rd sampling period, and 0.54 (95% CI = 0.45-0.63) in the 4th sampling period. We did not have age data for the first sampling period.

DISCUSSION

We detected a within-yr trend, and hence possible biases, in harvest-based CWD-prevalence estimates for both sexes, although the trend was steeper for males. Field data strongly suggest that the proportion of CWD-positive deer harvested increased across the three main sampling periods (rifle seasons) of each yr (Fig. 1) but not across yr. Bias in prevalence was greater for males than for females as indicated by the steeper within-yr slope on male estimates. For males, mean CWD prevalence was 5.4% when data were pooled across all sampling periods. The pooled estimate of 5.4% is relatively unbiased because it is within the 95% CI of prevalence estimates for any one sampling period. There was negligible bias in female estimates of prevalence when the data were pooled over all sampling periods. Consequently, we believe that pooling data over the four sampling periods resulted in relatively unbiased CWD-prevalence estimates and increased precision.

Although bias in CWD- prevalence estimates was small, the observed positive trend in CWD prevalence is interesting. CWD prevalence did not detectably increase over a period (1996–98). Thus, for

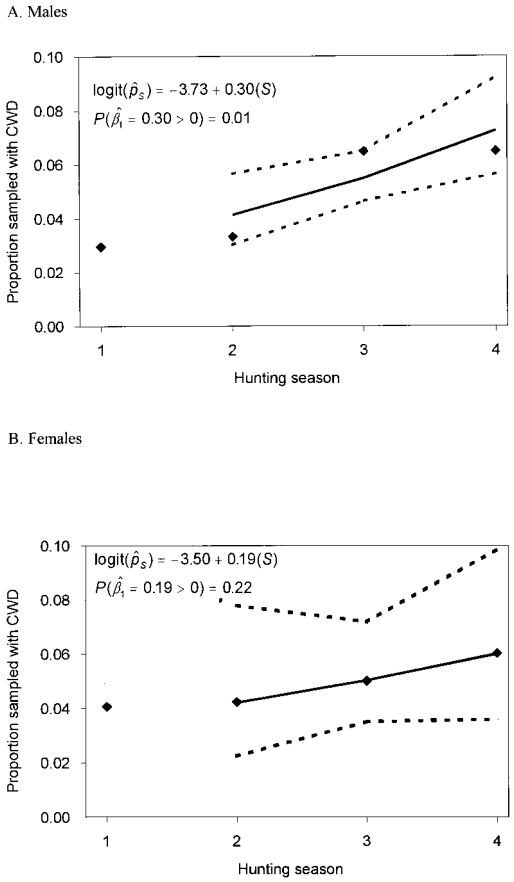

FIGURE 1. Observed (♦) and predicted (——) proportion of chronic wasting disease-positive (A) male and (B) female deer in game management units (9, 19, 191, and 20) in Larimer County, Colorado, sampled during 1996–98. Predicted values are based on the best model from Akaike's information criterion corrected for small sample sizes, which was a 3-rifle season trend model. *S* represents rifle-hunting seasons and dashed lines represent bounds of 95% confidence intervals on model predictions.

males the 2.9% increase in CWD prevalence over three sampling periods (Fig. 1A), which represents about seven weeks in time, is notable. On the surface, the observed trend appears most suggestive of CWD-infected deer being slightly less susceptible to harvest than uninfected deer during the early sampling periods, and becoming increasingly susceptible to harvest as the hunting season progresses. This result is counterintuitive to our original belief that, if anything, CWD-infected deer might be "easy targets" and thus be differentially more susceptible to harvest during the early sampling periods. Because the vast majority (97%) of test-positive deer detected in harvest surveys are preclinical CWD cases (Miller et al., 2000), hunter avoidance of sick individuals seems an unlikely explanation for the observed patterns. Rather than hunters avoiding preclinical CWD deer, it may be that preclinical deer exhibit behavioral symptoms, such as failure to learn, that make their susceptibility to harvest increase through time. To the extent that deer may learn to avoid hunters over the course of several hunting seasons, vulnerability to harvest should be most uniform during the first season each yr with selection against "slow learners" during each successive season. It follows that the increasing proportion of CWD-infected deer in successive seasons could reflect reduced learning capacity among CWD-infected individuals rather than reduced vulnerability to harvest during the early sampling periods.

Although it is possible that the positive trend was caused by increasing susceptibility of CWD-positive deer to harvest through time, other explanations are also plausible. One possible cause for within-yr trends is movement of deer between GMUs in conjunction with behavioral changes stimulated by the onset of the breeding season. Data were pooled across GMUs for analyses because sample sizes were not large enough to accurately estimate seasonal prevalence for each GMU. When data were pooled across season, CWD prevalence appears to differ among the four GMUs (Miller et al., 2000); the GMU with highest prevalence (9) also has the most restrictive hunter access and lowest overall harvest pressure (CDOW, unpubl. data). Movements of CWD-positive deer into areas where harvest was more likely may have occurred, particularly as the breeding season approached in early November during the third rifle-hunting season. As a result, the proportion of

CWD-positive deer in the sample could have increased between hunting seasons due to breeding-related movements.

If breeding season movements of deer from areas of high CWD prevalence caused the increase in proportion of CWD-positive deer during later sampling periods, then we speculate that older (≥3-yr-old) male deer will show this effect most acutely compared to other age or sex classes. Our speculation stems from the fact that older male deer, which are responsible for most of the breeding (Geist, 1981), may be more mobile, less wary, and hence more susceptible to harvest as the breeding season approaches. If this is true, then the proportion of older male deer harvested should increase as rut approaches, during sampling periods 3 and 4. Although the proportion of older deer harvested increased approximately 10% from sampling period 2 to 4, the increase was not significant. However, because prevalence is low, movement of a few CWD-positive male deer into areas where they are more likely to be harvested could cause the positive within-yr trend. We had too few data on male CWD-positive older deer ($n = 24$) to do viable analysis. However, in preliminary analysis, we found the proportion of older CWD-positive bucks harvested increased from 50 to 80% between sampling periods 2–4. Because of our low sample sizes, this trend was not significant. However, if future age data bear similar trends, we may find that older bucks, which have a higher prevalence of CWD than younger bucks (Miller et al., 2000), drive the within-yr trend in the data. Thus, breeding season movements remain a likely cause of the positive trend in proportion of CWD-positive deer harvested.

Another explanation for the positive trend in CWD prevalence is that disease progression is unidirectional through time, and observed trends may simply reflect progression, perhaps seasonal (Miller et al., 2000), in accumulation of detectable prion deposits in infected deer. However, the timeframe for such progression seems relatively short. Finally, variation in the data due to unknown factors may have produced this trend in the absence of bias (Joiner, 1982).

Although we had a large enough sample size (i.e., enough power) to detect bias, we point out that bias cannot be detected by AICc model selection, or any other model-selection method, when harvest rates are low due to insufficient data. Thus, failure to detect a trend would not mean that biases did not exist in the data, only that there was not a large enough sample size to detect the trend. Additionally, if susceptibility of CWD-infected deer was constantly lower than uninfected deer, a trend would not be detected. For example, if behavior were affected in CWD-positive deer such that these deer were always in hiding and had low probability of being shot throughout the four-season sampling period, then prevalence estimates would always underestimate true prevalence. Testing for this bias would require sampling in a totally different method that would capture infected and uninfected deer with equal probability (Courchamp et al., 2000).

Knowledge about differential susceptibility of diseased animals to hunting, or to any other control method, would be a valuable management tool for the design of disease eradication or control programs. Although we detected a slight bias in CWD-prevalence estimates from Colorado harvest data, we hesitate to conclude that differential susceptibility is truly the cause in light of the confounding factors discussed previously. AICc model selection is an initial step to detect bias in prevalence estimates from harvest data. But because of the many possible (and often unknown) contributing factors, model-selection methods may have limited utility for determining the factor that caused bias in prevalence estimates. If model selection suggests bias, then design-based methods (i.e., experimental manipulation) may be

the necessary next step in determining the cause of bias.

Although this methodology does not assign causality to bias, testing for bias is an important task in itself for several reasons. First, while we found our sample to be relatively unbiased. Other harvest samples, that rely on one hunting season for prevalence estimates, may contain serious bias. We caution against using one harvest season to estimate prevalence without initially testing for bias by estimating prevalence over several time periods. Second, identifying temporal trends will allow design of a sampling strategy to minimize bias, or allow bias to be accounted for in estimates. Third, detection of temporal prevalence trends may provide information about seasonal or annual patterns of a disease, illuminate epidemic properties of a disease, or suggest biological hypotheses that could further understanding of a disease (Courchamp et al., 2000). Fourth, managers concerned with controlling a disease through harvest may wish to know when infected animals, for whatever reason, are most or least likely to be harvested; trend data could provide the manager with this information. Finally, we point out that harvest sampling allows gathering of prevalence information at a low cost without having to remove additional animals from sampled populations.

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