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White-Tailed Deer Harvest From the Chronic Wasting Disease Eradication Zone in South-Central Wisconsin

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Abstract

*Chronic wasting disease (CWD) was discovered in free-ranging white-tailed deer (*Odocoileus virginianus*) in south-central Wisconsin in 2002. The current control method for CWD in the state is the harvest of deer from affected areas to reduce population density and lower CWD transmission. We used spatial regression methods to identify factors associated with deer harvest across south-central Wisconsin. Harvest of deer by hunters was positively related to deer density (slope = 0.003, 95% CI = 0.0001–0.006), the number of landowners that requested harvest permits (slope = 0.071, 95% CI = 0.037–0.105), and proximity to the area of highest CWD infection (slope = –0.041, 95% CI = –0.056– –0.027). Concomitantly, harvest was not impacted in areas where landowners signed a petition protesting intensive deer reduction (slope = –0.00006, 95% CI = –0.0005–0.0003). Our results suggest that the success of programs designed to reduce deer populations for disease control or to reduce overabundance in Wisconsin are dependent on landowner and hunter participation. We recommend that programs or actions implemented to eradicate or mitigate the spread of CWD should monitor and assess deer population reduction and evaluate factors affecting program success to improve methods to meet management goals.* (WILDLIFE SOCIETY BULLETIN 34(3):725–731; 2006)

Key words

chronic wasting disease, deer herd reduction, harvest, Odocoileus virginianus*, white-tailed deer, Wisconsin.*

Chronic wasting disease (CWD) is a fatal neurodegenerative disease that affects free-ranging and captive wildlife including elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*O. virginianus*; Miller et al. 2000). Chronic wasting disease has been found in free-ranging cervids in portions of Colorado, Nebraska, South Dakota, Wyoming, Saskatchewan, New Mexico, Illinois, Utah, Wisconsin, and New York (Joly et al. 2003). Transmission of CWD likely occurs through direct contact between infected and susceptible animals and indirectly through contact with an environmental source of infectious prions (Williams et al. 2002, Miller et al. 2004). Deer of all ages appear to be susceptible to CWD, and it appears the disease is ultimately fatal to all infected animals (Williams et al. 2002). Modeling studies (Gross and Miller 2001) suggest that high rates of CWD infection may cause a significant decline in deer populations by lowering adult survival, and failure to control the disease may lead to population declines. Regulated recreational hunting has become the primary mechanism used by wildlife managers for deer population control (Woolf and Roseberry 1998) and CWD management (Williams et al. 2002).

Chronic wasting disease was identified in free-ranging white-tailed deer in south-central Wisconsin in February 2002. Following the discovery of CWD in the Wisconsin white-tailed deer population, the Wisconsin Department of Natural Resources (WDNR) initiated a management program to eradicate CWD by harvesting deer from the CWD-affected area. A 1,809-km^2 disease eradication zone (DEZ) was established for CWD control in south-central Wisconsin (Fig. 1). Management goals in this zone included the harvest of as many deer as possible, including infected deer, in order to reduce the rate of CWD transmission, the potential for environmental accumulation of infectious prions, and the spread of CWD into adjacent areas (Bartelt et al. 2003).

Hunting seasons in the DEZ were extended (running from Sep through Mar) and an earn-a-buck program was implemented to increase antlerless (female) harvest. Most of the land in the DEZ (>90%), however, is privately owned. Brown et al. (2000) pointed out that privately owned lands have the potential to become refugia for deer (and disease) due to restricted hunter access and, thus, harvest. To increase landowner and hunter participation in the deer harvest effort, free harvest permits were offered to landowners in the DEZ.

Because of the large area over which CWD management in Wisconsin is being attempted and the reliance on recreational hunting, participation by both hunters and landowners in deer harvest is likely to be a key component to meeting management goals to reduce the deer population and control disease. The objective of our research was to identify factors that influence deer harvest and explain spatial patterns in deer harvest from the 2002 DEZ. We believe identification of factors that influence deer harvest will assist managers in developing strategies and harvest regulations likely to have the greatest impact on deer harvest and, thus, on their efforts to control CWD.

Methods

Study Area and Deer Density

During spring and summer 2002, the WDNR harvested and tested approximately 1,400 deer to obtain a preliminary assess-

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Figure 1. Location of the 2002 chronic wasting disease eradication zone (light gray) in south-central Wisconsin.

ment of the distribution of CWD infection in south-central Wisconsin. Based on this initial surveillance, a 1,809-km^2 (696 2.6-km^2 sections) DEZ encompassing all positive cases was established (Fig. 1). Our analysis included deer harvested from the DEZ during the 2002 harvest season (Sep 2002–Mar 2003). Hunters were required to register every deer harvested from the DEZ. Hunters were shown large-scale plat maps at registration stations and asked to identify the landowner on whose land they were hunting. Harvest locations were recorded to the Public Land Survey System unit "section" (2.6-km^2).

Deer were counted by the WDNR in a postharvest (14–19 Feb; 5 Mar 2003) helicopter survey of 100 randomly selected sections within the DEZ (R. E. Rolley, WDNR, unpublished data). Each survey was flown with 2 observers and a pilot. Each observer had at least 80 hours of helicopter survey experience and pilots had several hundred hours of previous deer survey experience. Observability of deer during these flights was estimated to be approximately 65%. We added autumn harvest to observability-adjusted deer counts to calculate preharvest (autumn 2002) deer density for each of the 100 surveyed sections.

We developed a linear model that predicted natural log (ln)-transformed preharvest deer density in each of the 100 surveyed sections as a function of the amount of deer range (suitable habitat for deer as defined by the WDNR) and location of each section north or south of a major highway (US-18/151) demarcating a change from primarily forested habitat to more fragmented, agricultural habitat. We used this linear model to estimate deer density for all nonsurveyed sections (based on deer range and location relative to US-18/151) within the DEZ. However, because deer range and section location do not perfectly predict deer density in the surveyed sections, this approach does not account for the error in the regression relationship.

To correctly characterize uncertainty (error) in the relationship between predicted deer density and deer harvest and to avoid finding a spurious correlation between these 2 factors (Schafer and Olsen 1998), we used multiple imputation, a robust statistical technique frequently used in medical and survey research (Rubin 1987, Schafer 1997, 1999, Schafer and Olson 1998) for incorporating uncertainty when predicting missing values in a data set (refer to Appendix A for a detailed explanation of this method), to estimate deer density for all sections within the DEZ. We generated 10 independent estimates of autumn deer density for each section in the DEZ using multiple imputation in the statistical program R (R Development Core Team 2004; mice package). These 10 imputed estimates provided a means of capturing the uncertainty in predicting deer density using our linear model. After performing multiple imputation, analyses of the relationships between estimated deer density, the covariates described below, and deer harvest were conducted.

Statistical Analysis

We focused our analysis on factors that might influence deer harvest or be related to CWD management and explain variation in the number of deer harvested from sections within the 2002 DEZ. Specifically, we evaluated whether deer density, landowner participation in or opposition to CWD control efforts, and proximity to CWD infection influenced the number of deer harvested from each section. To quantify landowner participation in CWD-control efforts, we used the number of landowners in a section that requested free antlerless harvest permits to reduce deer density or indicated they would permit WDNR personnel to harvest deer on their property. To quantify opposition to CWD management, we used the number of acres owned by individuals who signed a petition specifically protesting deer population reduction as a CWD-control strategy. We used a section's distance from the center of the area with highest CWD prevalence (core area; Joly et al. 2003; 0–34 km) to evaluate whether proximity to disease influenced deer harvest. We also tested for broad-scale spatial trends running north–south (total distance = 45.2 km) and east–west (total distance = 51.4 km) and for local spatial dependence (autocorrelation) in deer harvest among sections.

Spatial autocorrelation models can take either conditional or simultaneous forms that differ on how the spatially correlated error structure is specified (Haining 1990, Cressie 1993). We found similar results for both types of model, and we report results for only the simultaneous model. Specifically, we used simultaneous spatial autoregression (SAR), a technique that augments standard ordinary least squares regression (OLS) by accounting for local autocorrelation, following procedures similar to those described in detail by Lichstein et al. (2002). Briefly, we first fit an OLS model ignoring local spatial autocorrelation; we then conducted a Moran's I analysis (Cliff and Ord 1981; program R, spatial package) to test whether the OLS residuals were spatially correlated (i.e., whether the number of deer harvested from a section was correlated with the number of deer harvested from neighboring sections). The SAR analysis uses a neighborhood correlation matrix to incorporate local autocorrelation into the

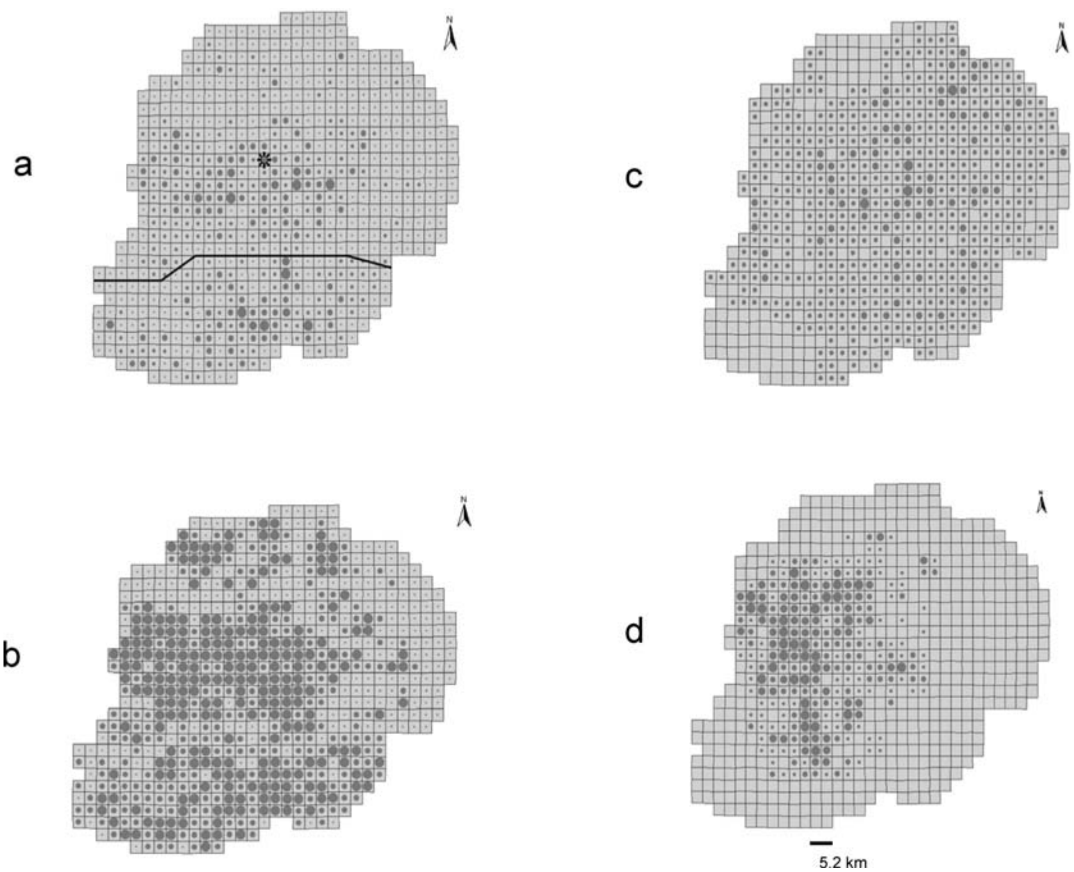

Figure 2. Dot-density plots of the number of (a) deer harvested, (b) mean imputed deer density, (c) number of landowners requesting harvest permits, and (d) acreage owned by petition signers, in each 2.6-km^2 section within the 2002 chronic wasting disease (CWD) eradication zone in Wisconsin. Increasing dot size is proportional to increasing magnitude of the measured quantity. Sections with no dot have a value of zero. In panel (a) the asterisk represents the center section of highest CWD prevalence (CWD core area) and the thick black line represents the location of highway US-18/151.

evaluation of the relationship between deer harvest and the covariates described above. Following SAR analysis, we conducted another Moran's I analysis to ensure local autocorrelation was successfully incorporated in the analysis. We performed all analyses using program R (spdep package).

We conducted SAR analyses of the relationship between deer harvest and the covariates 10 times, once for each of the deer density predictions generated through multiple imputation. For each of these 10 analyses, we evaluated the relationship between deer harvest and all covariate combinations (an all-possible-subset approach) and calculated model averaged parameter estimates and variances by weighting each coefficient (and associated variance) by Akaike weights (Burnham and Anderson 2002). We calculated final parameter estimates and their associated variances (across the 10 SAR analyses) following the methods described in Rubin (1987) and Schafer and Olsen (1998; Appendix A). We calculated standard errors and 95% confidence limits for each model parameter estimate and considered them significant if the 95% confidence interval did not include zero.

Results

During the 2002 deer harvest season, approximately 10,800 deer were harvested by hunters from the DEZ and registered with the WDNR. Harvest of deer, however, was highly heterogeneous across this region (range = 0–76 deer per section; Fig. 2a). Deer density also was highly variable (range = 0–154 deer per section; Fig. 2b). The number of landowners in a section who requested free antlerless harvest permits or indicated they would permit WDNR personnel to harvest deer on their property ranged from 0 to 14 landowners (Fig. 2c). Between 0 and 629 acres per section were owned by individuals who signed a petition specifically protesting deer population reduction as a CWD-control strategy (Fig. 2d).

Our linear model to predict preharvest deer densities in the 100 helicopter-surveyed sections explained 52.5% of variation in preharvest deer density (Table 1). Deer density was higher in sections with higher proportions of deer range, and there was an interaction between deer range and location north or south of US-18/151. Specifically, for sections with the same amount of deer range, deer range supported higher deer densities in sections in the more agricultural, fragmented habitat south of US-18/151 than north of the highway.

A Moran's I test of the OLS residuals indicated significant correlation in deer harvest among sections separated by <2.6 km (first- and second-order neighbors; $I = 9.806$, $P \leq 0.001$). Following each of the 10 SAR analyses, Moran tests were not significant (all $P > 0.05$), indicating that the spatial dependence among sections was successfully accounted for. Model-averaged results from the 10 SAR analyses based on the imputed data sets indicated that deer density, the number of landowners who requested harvest permits, and distance from the CWD core area

Table 1. Parameter estimates and standard errors (SE) for the regression relationship between deer density (natural log transformation) and deer range and location north or south of highway US-18/151 in 100 aerial-surveyed sections in the 2002 chronic wasting disease eradication zone in south-central Wisconsin. $R^2 = 0.525$.

Parameter	Estimate	SE	*P*
Intercept	0.444	0.030	0.146
Deer range	0.038	0.004	≤0.001
South of US-18/151	2.090	0.540	≤0.001
Interaction	−0.021	0.008	0.013

Table 2. Model-averaged parameter estimates, standard errors (SE), and 95% confidence intervals (CI) for each covariate included in the simultaneous spatial autoregression analysis of the number of deer harvested per section (natural-log transformation) from the 2002 chronic wasting disease eradication zone in south-central Wisconsin calculated using the method described by Rubin (1987).

Parameter	Estimate	SE	95% CI[a]
Intercept	3.570	0.207	3.155–3.984
Deer density	0.003	0.001	0.0001–0.006
Landowner permits	0.071	0.017	0.037–0.105
Petition acreage	−0.00006	0.0002	−0.0005–0.0003
Distance from core	−0.041	0.072	−0.056– −0.027
East–West trend	−0.009	0.007	−0.023–0.005
North–South trend	−0.032	0.007	−0.045– −0.019

[a] Covariates whose 95% confidence intervals did not overlap zero were considered significant.

were significantly related to the number of deer harvested from a section (Table 2). Specifically, deer harvest increased with increasing deer density (Fig. 2b) and when more landowners requested harvest permits (Fig. 2c). In addition, deer harvest was highest in sections closest to the CWD core area and declined with increasing distance from the core. We also found a significant broad-scale trend indicating that deer harvest was higher in sections in the southern DEZ relative to the northern part of the zone. Acreage owned by individuals who signed a petition opposing intensive deer population reduction to control CWD did not impact deer harvest (slope = −0.00006, 95% CI = −0.0005–0.0003, Fig. 2d).

To further validate the relationship between deer harvest and deer density (because deer habitat and location were used to estimate deer density), we repeated our analysis using only the 100 sections where deer density was estimated through aerial survey counts. This analysis confirmed that deer density itself was positively related to deer harvest (slope $= 0.017$, $P \leq 0.001$).

Although we did not evaluate an exhaustive list of potential variables, several covariates that we considered were significantly related to deer harvest. To facilitate interpretation of the effect of each covariate on deer harvest, we calculated the relative change in deer harvest based on a range of covariate values observed in the DEZ. The median number of landowner permits (2 permits) per section resulted in a 15% increase in the number of deer harvested relative to sections where no landowner permits were issued and a 53% increase for sections where 6 landowners requested permits (90th percentile). The median deer density (36 deer/section) resulted in a 9.5% increase in deer harvest relative to the 10th percentile of deer density (4 deer/section). Sections in the DEZ with high deer density (90th percentile = 62 deer) resulted in only a 19% increase in deer harvest compared to harvest at the 10th percentile of deer density. Deer harvest declined substantially with increasing distance from the core area: 50% reduction at the median distance (16.8 km) and 66% reduction at the 90th percentile (26 km).

Discussion

We identified several factors associated with deer harvest from the chronic wasting disease eradication zone in south-central Wisconsin. Harvest of deer from 2.6-km^2 sections in the DEZ was positively correlated with the number of deer harvested from neighboring sections (8 adjacent sections). Spatial correlation in deer harvest may indicate that anthropogenic and ecological processes affecting deer harvest are operating at scales larger than 2.6 km^2. The presence of local autocorrelation also is an indication that ecological and sociological factors not included in our analyses likely influence deer harvest. Wildlife managers have long relied on recreational harvest to reduce deer population numbers (Woolf and Roseberry 1998). Future research is needed to identify additional factors not measured in this study that may be influencing deer harvest, especially in relationship to population reduction for management of disease (Wobeser 2002).

Deer harvest was higher from sections in the southern part of the DEZ relative to areas further north. Deer habitat in the DEZ changes from somewhat fragmented, mixed agricultural–forest habitat in the south to more forested habitat in the north. In Illinois, Foster et al. (1997) found that deer in counties with small amounts of fragmented forest cover were more susceptible to harvest than were deer in counties composed of contiguous forest. The higher harvest of deer from fragmented habitats may have implications for deer harvest of deer harvest from the newly discovered CWD-infected deer population in the highly fragmented landscape of southeastern Wisconsin and northern Illinois.

We found that more deer were harvested from sections with high deer densities relative to those with lower deer densities. A positive relationship between deer harvest and deer density has previously been reported (Holsworth 1973). In Illinois, for example, both daily and annual harvests were positively related to estimated deer population density (Hansen et al. 1986). We recommend that future research also consider the relationship between deer density and the proportion of the deer population harvested to evaluate how density, hunter effort, and other factors influence deer harvest. Improved knowledge of the functional relationship between these factors will assist in developing disease or overabundance programs where a significant reduction in deer abundance is required.

Proximity to the CWD core area also was related to the number of deer harvested. We hypothesize that the larger number of deer harvested from sections closer to the CWD core area reflects increased awareness of the disease, resulting in greater effort to eliminate deer with the highest risk of CWD infection. Additional human dimensions research is necessary to understand the relationship between perception of disease risk and the participation of hunters and landowners in the management effort.

Independent of geographic location, we found that deer harvest was positively associated with landowner participation in WDNR CWD-control strategies. Specifically, deer harvest increased as the number of landowners who requested harvest permits or allowed WDNR personnel to harvest deer on their land increased. Restricted hunting on private lands could lead to refugia for deer that will affect harvest distribution, reduce the ability to control deer populations (Brown et al. 2000), and create potential disease foci. Efforts by WDNR to communicate with landowners about CWD management and to offer programs that increase landowner participation and increase deer harvest should be encouraged.

Unlike the trend in deer harvest related to increasing landowner participation, deer harvest was not related to the acreage owned by individuals who signed a petition opposing intensive deer population reduction as a strategy to control CWD. There are, however, groups of citizens and hunters in Wisconsin who continue to be opposed to intensive deer population reduction for CWD control. Research to identify messages that will be effective in gaining support from the public for wildlife management strategies such as hunting is necessary (Campbell and MacKay 2003).

A variable we were unable to measure that is likely to impact deer harvest and control of CWD is hunter access to private land for hunting. Because most of the land in the DEZ is privately owned, land access for hunting is likely to be an important constraint to reducing deer densities. Lack of access to private land could potentially create refugia for infected deer or prion-contaminated environments. As deer densities are further reduced, harvest of deer may become increasingly difficult (VanDeelen and Etter 2003). In addition, Brown et al. (2000) suggested that recreational hunting alone is unlikely to bring about large changes in deer populations across broad landscapes. A model developed by Nugent and Choquenot (2004) simulated the cost-effectiveness of various harvest methods to reduce deer populations in New Zealand and found that major reductions in deer density were unlikely to be achieved through recreational hunting alone. Development of additional strategies to effectively reduce deer population abundance and, thus, control CWD may be necessary.

Management Implications

The objective of our study was to identify factors related to hunter harvest of deer in the chronic wasting disease eradication zone of south-central Wisconsin. Our results indicated that hunters harvested more deer in sections where deer were more abundant, in sections where disease was more prevalent, and in sections where more landowners requested harvest permits.

Recreational deer harvest is the main method being used to control CWD in south-central Wisconsin and some other states (e.g., Colorado) and provinces (e.g., Saskatchewan; Williams et al. 2002). Deer population reduction is designed to reduce disease transmission and prevalence, reduce the accumulation of infectious prions in the environment, and prevent the spread of the disease to deer in adjacent areas. A key component of adaptive management is to monitor management actions, evaluate their success, and adjust management efforts appropriately (Lee 1993). Wisconsin is taking a similar, though less formalized approach to managing CWD.

Recreational hunting also continues to be the primary mechanism used by wildlife management to reduce the size of white-tailed deer populations (Woolf and Roseberry 1998). Managers can regulate harvest by controlling factors such as the duration of the hunting season, harvest limits, sex restrictions, and equipment used. Factors that affect hunter behavior and efficiency, however, are more difficult to understand. Given the long-term trends of declining hunter participation and increasing hunter age (U.S. Department of the Interior 2002), reliance on recreational harvest to reduce deer population numbers to reduce overabundant populations or to control disease will continue to be a major challenge for wildlife managers into the future.

Brown et al. (2000) stressed that management agencies would benefit from an identification of those factors that motivate hunters and that will be key to meeting population reduction goals. The results of studies such as ours or, for example, by Stedman et al. (2004), who examined hunter behavior and its relationship to variables such as hunter motivation, attitudes, and experiences, can be used by wildlife managers to develop management strategies designed to maximize deer harvest.

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Appendix

Description of the multiple imputation technique for the estimation of missing data

Multiple imputation is a technique applied to incorporate uncertainty into estimates of missing values in a data set (Rubin 1977, 1987). Simply substituting mean values for unknown data will dampen relationships among variables, while using regression predictions will artificially inflate relationships because uncertainty is ignored (Schafer and Olsen 1998). The multiple imputation approach entails 4 main steps: 1) specifying a posterior predictive density distribution based on the relationship between observed data and a set of predictor variables; 2) drawing imputations from the predicted distribution to produce m complete data sets; 3) performing m standard data analyses (simultaneous spatial autoregression in this article); and 4) pooling the results of the m analyses for calculation of final parameter and variance estimates. Detailed descriptions of these steps are provided below.

In a multiple imputation approach, missing values are replaced by a set of $m > 1$ plausible values. One multiple imputation method employs Bayesian linear regression and Markov Chain Monte Carlo methods to estimate missing data based on the relationship between observed data and other known variable(s) (Schafer 1999). This method incorporates variance in the regression relationship by using independent values (imputations) drawn from their predictive posterior distribution (in our case an assumed multivariate normal distribution derived from the regression relationship between observed deer density and deer range and location north or south of US-18/151) for estimates of missing data (VanBuuren et al. 1999).

Once multiple imputation has been conducted, there are now m complete data sets. The data sets can be analyzed using the statistical methods appropriate to the data. The estimated coefficients and standard errors resulting from statistical analysis on each of the m data sets can be combined following the rules of Rubin (1987) to obtain overall coefficient and variance estimates that will be used to calculate 95% confidence intervals and evaluate parameter significance. Specifically, the overall estimate ($\bar{Q}$) for each parameter is the arithmetic average of the m estimates ($Q_1, Q_2, \ldots, Q_m$) given by the equation

$$\overline{Q} = \frac{1}{m}\sum_{i=1}^{m} Q_i.$$

Total variance for each parameter is composed of 2 components accounting for variability within and across data sets. Within-imputation variance ($\bar{U}$) is the average of the estimated variances from each imputation ($U_1, U_2, \ldots, U_m$)

$$\overline{U} = \frac{1}{m}\sum_{i=1}^{m} U_i,$$

and between-imputation variance is the sample variance of the estimated parameters

$$B = \frac{1}{m-1}\sum_{i=1}^{m}(Q_i - \overline{Q})^2$$

(Schafer and Olsen 1998). Total variance is, therefore, given by the equation

$$T = \overline{U} + \left(1 + \frac{1}{m}\right)B.$$

A practical advantage of using multiple imputation to estimate missing data is that, unlike bootstrapping, multiple imputation methods achieve highest efficiency after only 5–10 imputations, depending on the proportion of missing data (Schafer 1999).

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