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Articles

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Abstract

Local and regional land use changes, such as the expansion of cropland for cellulosic biofuels, and the population density of white-tailed deer can affect the health and body mass of white-tailed deer *Odocoileus virginianus*. We collected hunter-harvest data for 1,731 white-tailed deer from DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa from 2003 to 2010. We used linear mixed-effects models and information theoretic methods to estimate effects of density of white-tailed deer and proportion of total landcover area converted from cropland to cool- or warm-season grassland on body mass of white-tailed deer. Density of white-tailed deer at DeSoto National Wildlife Refuge ranged from 36.5 to 50.6 deer/km², and the proportion of landcover at DeSoto National Wildlife Refuge that remained cropland each year ranged from 14.9 to 23.2%. Body mass was inversely related to population density (-1.4 kg/5.5 deer/km²) and proportion of cropland (-1.3 kg/3.1% conversion of total land area from cropland to grassland). We used auxiliary harvest data collected at Boyer Chute National Wildlife Refuge to validate our models and found our models performed well. We estimate densities of white-tailed deer must be reduced by 1.7 (SE = 0.6) deer/km² for every 1% change in total landcover from cropland to grassland in order for white-tailed deer to maintain body mass. Our results indicate increased harvest of white-tailed deer, resulting in a reduction in population density, may offset negative effects that a decline in the amount of available cropland could have on the body mass and health of white-tailed deer.

Keywords: biofuels; body condition; cropland; density dependence; DeSoto National Wildlife Refuge; grassland; white-tailed deer

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Introduction

White-tailed deer *Odocoileus virginianus* (hereafter deer and white-tailed deer are used interchangeably to refer to *O. virginianus*) are the most numerous and most

often hunted species of big game in North America and are of considerable interest to managers, landowners, and sportspersons alike (McShea et al. 1997; Côté et al. 2004). In general, the body mass of white-tailed deer varies temporally with marginal effects such as weather,



forage availability associated with land use, and population density (Nixon et al. 1970; Kie et al. 1983; DelGiudice et al. 1992; Garroway and Broders 2005; Simard et al. 2010). Estimating marginal effects of major determinants of body mass is a prerequisite for determining appropriate management actions for controlling the health of white-tailed deer when one or more of the determinants of body mass is dynamic. Accurate estimates of marginal effects of body mass could be used to estimate harvest rates that would allow managers to maintain body mass of deer.

In many areas, agricultural crops are a superior source of food for white-tailed deer, and the amount of available cropland may influence body mass of deer (Nixon et al. 1970; Johnson et al. 1987; Tonkovich et al. 2004). With advancements in the methods of biofuel production, however, conversions of agricultural cropland to cool- or warm-season grasslands for biomass production may be forthcoming, and it is likely that such conversions would have a negative effect on body mass and health of deer (Bies 2006; Dicks et al. 2009; Walter et al. 2009; Dale et al. 2010). Alternatively, high commodity prices and current reduction of Conservation Reserve Program lands could potentially result in an increase in the amount of cropland (Secchi et al. 2009; Dale et al. 2010; Farm Service Agency [FSA] 2010). In both scenarios, the effects of land use change on the health of white-tailed deer is unknown, and managers need more precise tools to manage deer in the face of changing land use patterns.

In addition to the amount of available cropland, population density of deer can be a major determinant of health and body mass of white-tailed deer (Kie et al. 1983; Shea et al. 1992; Sams et al. 1998; Keyser et al. 2005). Unbiased estimates of the marginal effects of population density on body mass of deer can be difficult to obtain because accurate and unbiased estimates of population abundance are needed. Keyser et al. (2005) used population reconstruction methods to estimate population densities and reported a density-dependent response in body mass of white-tailed deer. Population reconstruction methods, however, are not robust to dynamic harvest regimes or widely fluctuating population densities that typically occur, and therefore estimates of the marginal effect of density may be biased (McCullough 1979; Roseberry and Woolf 1991; Jacobsen 1992; Skalski et al. 2005). A complete census using helicopter surveys may be more accurate than population reconstruction methods if a dynamic harvest regime occurs or the population fluctuates widely (Beringer et al. 1998).

Studies documenting relationships between body mass and density of white-tailed deer have generally used a hypothesis-testing paradigm and single, fixed-effect linear regression analyses (Kie et al. 1983; Keyser et al. 2005). Interpretation of the relationships between body mass and density of deer using these approaches, however, may be uninformative if other determinants of body mass, such as the amount of available cropland, are not constant or cannot be modeled as residual error. In these cases, a hypothesis-testing approach may be inappropriate because the response in body mass caused by a change in deer density may be subtle, confounded,

and difficult to detect, especially if land use changes are ignored (Anderson et al. 2000). It is unknown, however, if a single fixed-effect model best described the data in past studies because models containing additional determinants of body mass were not evaluated (Keyser et al. 2005). An information theoretic approach allows one to test multiple working hypotheses, which may be more appropriate if determinants of body mass of deer are multidimensional and change through time (Anderson et al. 2000; Burnham and Anderson 2002).

Several indicators, such as reproductive success, body mass, and various measurements of stored fat such as in kidney or bone marrow, may be used to measure health of deer (DelGiudice et al. 1990; Sams et al. 1998; Cook et al. 2010). Many local managers and state agencies collect data on sex and age of harvested deer, but few collect body mass measurements. For management purposes, such as maintaining healthy deer in a population, body mass is one of the simplest forms of body condition data and can be easily collected along with other hunter-harvest data such as sex and age. Here we examined marginal effects of population density and proportion of total land area used for cropland production on the body mass of white-tailed deer and estimated harvest rates that would allow managers to maintain body mass of deer when population density or landcover composition change. Our results provide managers with a quantitative starting point for an adaptive harvest management plan to manage the health of white-tailed deer.

Study sites

Our study was conducted at DeSoto National Wildlife Refuge (DNWR), which was located 30 km north of Omaha, Nebraska, in the Missouri River Valley of eastern Nebraska and western Iowa, from 2003 to 2010. The DNWR was a 2,935-ha mosaic of forest, cropland, grassland, aquatic habitat, and 452 ha of river and oxbow lake habitat. Deciduous forest was the dominant (47%) land cover, and the overstory was dominated by mature eastern cottonwood *Populus deltoides*. The understory included rough-leaved dogwood *Cornus drummondii*, hackberry *Celtis occidentalis*, mulberry *Morus rubra*, and green ash *Fraxinus pennsylvanica*. The ground layer was dominated by poison ivy *Toxicodendron radicans* and common scouring-rush *Equisetum hyemale*. The average amount of cropland at DNWR during the study was 19.9% (Table 1). Crops such as alfalfa, corn, sorghum, soybeans, alfalfa, and a mix of wheat and clover were cultivated on a 3-y rotation. Alfalfa, clover, sorghum, and 10–16% of the corn crop was left standing each winter as food plots for wildlife. The area surrounding DNWR was predominantly cropland and similar riparian vegetation. Although annual crop rotations occurred on neighboring properties, the surrounding area had not experienced large-scale changes in land use. White-tailed deer was the only large herbivore in the study area. Soils were in the Albaton-Hayne association (Natural Resource Conservation Service [NRCS] 2006), and the topography was relatively flat with slopes $\leq 2\%$ (U.S. Department of Agriculture [USDA] 1976). Average annual maximum and minimum temperatures from 1971 to 2000 were 15.4 and

Table 1. Percent of total land in the study area used as cropland, number of white-tailed deer *Odocoileus virginianus* per square kilometer harvested by hunters, estimates of density of deer (deer/km²) obtained using a post-hunt helicopter count, and estimates of pre-hunt population density (harvest plus helicopter count) at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2003–2010.

Year	% Cropland	Hunter harvest	Post-hunt count	Pre-hunt density
2003	23.2	7.9	33.5	41.4
2004	20.0	14.9	31.6	46.5
2005	20.9	23.8	26.8	50.6
2006	20.4	22.1	24.4	46.5
2009	14.9	10.2	26.3	36.5

3.4°C, respectively (NRCS 2005). Average annual precipitation in the form of rain was 760 mm, and average annual snowfall was 750 mm (U.S. Fish and Wildlife Service [USFWS] 2001).

In accordance with the National Wildlife Refuge System Improvement Act of 1997 (Public Law 105-57 1997), staff of DNWR prepared a Comprehensive Conservation Plan (CCP) in 2001 to specify a direction for management of the refuge (USFWS 2001). The CCP proposed that 75% of the cropland be reverted to native vegetation by 2015. Previous conversions of cropland to native vegetation had occurred from 1991 to 2002 when approximately 4% of cropland was removed annually and replaced with native vegetation. Most conversions of cropland (>95%) were to cool- and warm-season grasses including: smooth brome *Bromus inermis*, western wheatgrass *Pascopyrum smithii*, big bluestem *Andropogon gerardii*, little bluestem *Schizachyrium scoparium*, Indiangrass *Sorghastrum nutans*, switchgrass *Panicum virgatum*, and side oats grama *Bouteloua curtipendula*.

Additional research was conducted on the island portion of Boyer Chute National Wildlife Refuge (BCNWR). The island portion of BCNWR was a 790-ha area located 7 km downriver from DNWR that had similar soil, topography, climate, and native vegetation structure. All crop fields at BCNWR were converted to native grassland during 1993–2002. Prior to conversion, BCNWR was approximately 60% cropland.

Methods

Data collection

We collected data on sex, age, field-dressed body mass, and date of harvest for 1,731 white-tailed deer harvested by hunters at DNWR from October 2003 to January 2007 and October 2009 to January 2010 and 66 white-tailed deer harvested by hunters at BCNWR from October 2004 to October 2005. Two-day either-sex deer hunting seasons occurred in early December and 2-d antlerless deer hunting seasons occurred in early and late October and early January at DNWR. Two-day antlerless deer hunting seasons occurred in October at BCNWR during 2004 and 2005. Either-sex deer hunting seasons

permitted the harvest of any female or male deer and antlerless deer hunting seasons permitted the harvest of female deer and male deer with <15-cm antlers. We grouped harvest data collected during January with data collected during fall hunting seasons of the previous year. In an attempt to decrease the population of antlerless deer at DNWR, the number of permits issued in the hunting unit increased from 270 permits in 2003 to 1,470 permits in 2006. Data collected at BCNWR were only used to validate models developed with data collected at the DNWR.

A group of seven trained biologists with access to known-age jaw sets from the study area determined age by tooth eruption and wear and categorized deer as 0.5, 1.5, 2.5, 3.5, 4.5–5.5, 6.5–8.5, and 9.5+ y of age (Severinghaus 1949). We combined deer ≥4.5 y of age in our analyses because age differentiation by tooth wear becomes increasingly difficult, and maximum mass typically was reported to be attained by this age (Roseberry and Klimstra 1975; Hamlin et al. 2000). We measured mass of harvested deer to the nearest 0.45 kg (1 lb). Our data, as well as covariates used in our analysis, can be found in the *Supplemental Material* (Data S1).

We used a Robinson R44 helicopter flown at an altitude of 100–200 m and at speeds of 30–60 km/hr with the same observer to count deer in the study area each year. We conducted helicopter surveys in a manner similar to Beringer et al. (1998) after the final hunt of the year and when snow accumulation was ≥12 cm. We conducted helicopter surveys at BCNWR and DNWR on the same dates with the same observer. Most deer were located in forested areas that were linear or small in size, which created natural transects for conducting surveys. Detailed maps documenting our helicopter survey for each year are available in the *Supplemental Material* (Data S2). We estimated our primary measure of pre-hunt density of deer by adding counts of deer obtained through helicopter surveys to the number of deer harvested during the preceding hunting seasons (Table 1). We estimated a secondary measure of density using helicopter counts plus annual recruitment to check the accuracy of our primary source. We estimated fawn-to-doe ratios and proportion of does in the adult population by observing deer with binoculars and spotting scopes in nonforested areas from approximately 1 h before sunset until dusk from August through early October. We estimated annual recruitment using post-hunt helicopter surveys multiplied by the subsequent year's fawn-to-doe ratio and proportion of does in the adult population. Post-hunt helicopter counts plus recruitment should predict the subsequent year's primary estimate of pre-hunt density if immigration, emigration, and non-hunting-reported mortality are negligible or if these sources of bias are compensatory.

We used annual landcover maps produced by DNWR staff to calculate the proportion of cropland converted to cool- or warm-season grassland and the proportion of DNWR that remained cropland each year (Table 1). Maps produced by refuge staff detailing habitat types and amount of cropland for BCNWR are available in the *Supplemental Material* (Data S3). We calculated the

relative change in amount of cropland by subtracting the maximum proportion of cropland from the minimum proportion of cropland and dividing by the average proportion of cropland.

Data analyses

We constructed nine a priori linear mixed-effects models using covariates based on biological relevance determined from a review of scientific literature (Table 2; Burnham and Anderson 2002). Explanatory fixed-effect covariates, followed in parenthesis by variable name, included sex (sex), age class (age), pre-hunt density estimates (density), and proportion of total landcover area that was cropland (crop). We tested covariates density and crop for correlation and determined they were highly correlated ($R^2 = 0.64$; Neter et al. 1996). We did not take explicit remedial measures to adjust for collinearity of predictor variables because it was not clear that such measures were in fact remedial (Smith et al. 2009); we discuss the impacts of collinearity in the interpretation of our results. We standardized continuous variables (density and crop) so that each had a mean of 0.0 and a standard deviation of 1.0.

Model formulae outlined below include symbols “+” that indicates inclusion of main effects and “*” which indicates inclusion of main effects and an interaction between main effects. Our most parsimonious model, other than an intercept-only null model, was sex*age because differentiation of body mass based on sex and age was previously established (Roseberry and Klimstra 1975; Strickland and Demarais 2000). Density affected sex and age classes of deer differently in other areas of North America, so we included sex*age*density in our set of models to test the effect of density on body mass for each sex and age class of deer (Kie et al. 1983; Leberg and Smith 1993; Keyser et al. 2005). We considered the more general model, sex*age+density, because density may have an effect of equal magnitude on all individuals, which could occur with scramble competition (McCullough 1979). Nixon et al. (1970) and Johnson et al. (1987) reported availability of agricultural crops affected body mass of deer, but the effect varied by sex, age class, and the amount of corn in their diet. We also considered the hypothesis that mass of deer declined in response to replacing cropland with cool- and warm-season grassland with the models sex*age+crop, and sex*age+density+crop in addition to sex*age+sex*density+sex*crop, which assumes density and crop affected males and females differently, but did not affect age classes differently. We also included models sex*age*crop and sex*age*density+sex*age*crop in the set of models to test for an effect of crop on each sex and age class. We did not consider models that included only one interaction effect of density and crop on sex and age, such as sex*age*density+crop. Hypotheses that have age- or sex-specific effects for either density or crop but not for both variables seem unwarranted. More logically, both the effects of density and crop were sex- and age-specific; however, the ability of our data to discriminate between the global model and less complex models was the focus of our analysis.

In addition to multiple models for fixed effects, we considered four different random-effects structures for the random-effects model components. Our most parsimonious random-effects structure represented correlation among deer harvested during the same month nested within year (month(year)). As we might expect, the temporal variability in body mass may be different for male and female deer, and this constant correlation structure was likely overly simple. We therefore considered a random-effects structure that assumed body mass of deer harvested in the same month may be expected to be correlated, but the correlation also depends on sex (sex*month(year)). Our third model was simply a repeat of sex*month(year), but assumed a covariance between random effects. Our fourth model had the most complex correlation structure and included a random effect for each sex and age class combination with each month nested with year (age*sex*month(year)). The four random-effects models involve estimating 1, 2, 3, and 11 additional variance components for each fixed-effects model, respectively.

Since maximum likelihood (ML) underestimates the variance component of a mixed-model (Littell et al. 2006), we estimated variance components using restricted maximum likelihoods (ReML). Although ReML was the superior estimation method for variance components, likelihoods and likelihood-based information criteria are not comparable for fixed effects in the model; therefore, model selection occurred separately for fixed- and random-effects because no universal information criteria existed for simultaneous selection of both fixed and random effects (Grevén and Kneib 2010). We used Akaike's information criterion (AICc) adjusted for finite sample size for model selection based on the marginal likelihood (Grevén and Kneib 2010). We selected the random-effect components first using AICc based on ReML estimation. We selected the AICc best random-effects model and proceeded with fixed-effects model selection and multi-model inference using ML estimation methods to calculate AICc values. Although this model selection procedure does not result in multi-model inference for random effects, it was used for two reasons: 1) it was likely that the AICc best random-effects model would completely dominate model averaging and 2) methods were not well developed for model-averaging random effects. We calculated AICc weights (w), which could be interpreted as the weight of evidence that the model was the best approximation of truth given the data and that one of the models in the candidate set was the Kullback–Leibler best model (Burnham and Anderson 2002).

We performed model-averaging techniques across all fixed-effect model parameters to estimate the expected value and standard error. Model-averaged estimates assumed that coefficients not in the model were 0. We refrained from reporting model averaged parameter estimates that were 0. We estimated model-averaged standard errors using the unconditional variance estimator and covariance using the unconditional covariance estimator (Burnham and Anderson 2004). We used the delta method to estimate standard errors of functions of parameters (Powell 2007). Confidence intervals (CIs) and prediction intervals (PIs) were constructed using the

Table 2. A priori models used to estimate field-dressed body mass of white-tailed deer *Odocoileus virginianus* with log likelihood values (LL), number of parameters (K), Akaike's information criterion corrected for finite sample size (AICc), delta AICc values, AICc weights (w), and coefficient of determination (R^2) at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2003–2010.

Model ^a	LL	K	AICc	Δ AICc	w	R^2
Sex*age+density+crop	−5,346	16	10,725.10	0.00	0.700	0.800
Sex*age+sex*density+sex*crop	−5,346	18	10,729.04	3.94	0.098	0.800
Sex*age+density	−5,350	15	10,729.52	4.42	0.077	0.799
Sex*age	−5,350	14	10,729.56	4.46	0.075	0.799
Sex*age+crop	−5,350	15	10,731.08	5.98	0.035	0.799
Sex*age*density	−5,342	24	10,733.05	7.94	0.013	0.800
Sex*age*density+sex*age*crop	−5,334	34	10,737.08	11.97	0.002	0.802
Sex*age*crop	−5,349	24	10,746.15	21.05	0.000	0.799
Null model ^b	−6,737	5	13,484.44	2,759.34	0.000	0.000

^a All models contain a random effect of month and year harvested for each sex.

^b Null model fitted with an intercept and random effects.

equal-tailed normal approximation. We calculated a correlation coefficient (R^2) for the fixed effects to measure predictive power of each model (Edwards et al. 2008). This method, which was different from standard correlation coefficients used for fixed-effect-only models, assumes that the null model, which included all random effects, had an R^2 of 0. We examined residuals for normality and uniform variance (Neter et al. 1996; Littell et al. 2006).

We used our models from DNWR to predict the mass and 95% PIs of deer harvested at BCNWR. We plotted predicted and observed masses of deer from BCNWR with 95% PI for female deer harvested during the 2004 and 2005 seasons. We calculated the average difference between predicted and observed body mass for each sex and age class. We excluded male deer ≥ 1.5 y of age from the calculated differences because the seasons at BCNWR were for antlerless deer only and it was likely any legal male deer ≥ 1.5 y of age harvested in this antlerless season would provide a biased body mass. We used program R to conduct all statistical analyses (R Development Core Team, Vienna, Austria, <http://www.R-project.org>).

Results

The proportion of total land area in cropland production at DNWR decreased during our study from a high of 23.2% in 2003 to a low of 14.9% in 2009 (Table 1). Overall, this represented a 41.8% relative change in the amount of cropland. Hunters harvested an average of 15.8 deer/km² during the study period. We counted an average of 28.5 deer/km² during helicopter surveys conducted in February 2004, February 2005, March 2006, January 2007, and February 2010 (Table 1). We estimated the average pre-hunt density of white-tailed deer at DNWR to be 44.3 deer/km² (36.5–50.6 deer/km², Table 1). The relative change in density of deer was 31.8%. Annual estimates of recruitment were 29.1, 31.0, and 23.5 deer/km² for 2004, 2005, and 2006, respectively. Annual recruitment could not be estimated for 2003 and 2009 because all necessary data were not available. Density estimates based on post-hunt helicopter counts

from the previous year plus recruitment was 62.6, 62.6, and 50.3 deer/km² for 2004, 2005, and 2006, respectively. The mean difference between the pre-hunt density estimates and our population estimate based on post-hunt helicopter counts plus recruitment was −10.6 deer/km² (SE = 6.3).

The best random-effects model for explaining correlation among body mass of deer had three variance components and consisted of a correlated sex-specific random effect for month nested within year. The covariance of this model structure had a Δ AICc value of 7.3–12.3 (range for all nine a priori models) compared with the model with only a random effect of month nested within year, a Δ AICc value of 9.2–11.7 for the uncorrelated sex-specific random effect for month nested within year, and a Δ AICc value of 7.4–22.6 compared with the model with a sex- and age-specific random effect of month nested within year. The Δ AICc for the random effects corresponded to a $w > 0.95$ for the best random-effect model. The best model for predicting mass of white-tailed deer at DNWR contained the fixed effects sex*age+density+crop ($w = 0.700$, Table 2). The best model along with models sex*age+sex*density+sex*crop, sex*age+density, and sex*age accounted for $\geq 95\%$ of the AICc weight of evidence and had a similar coefficient of determination ($R^2 = 0.799$ –0.800; Table 2).

Male white-tailed deer were heavier than females of the same age class (Figures 1 and 2; Table 3). Females attained 95% of maximum body mass by 3.5 y of age and males attained maximum mass in the ≥ 4.5 -y age class at the mean population density (44.3 deer/km²) and mean amount of cropland (19.9%) at DNWR during our study. The amount of available cropland at DNWR did not influence the age at which deer obtained maximum mass. Predictions obtained from our models indicated that at 5.0% cropland, which was the management goal for DNWR, both females and males would reach 95% of maximum mass at 3.5 and 4.5 y of age, respectively (Figure 1).

After standardizing variables density and cropland, a 1-unit increase in density of white-tailed deer was

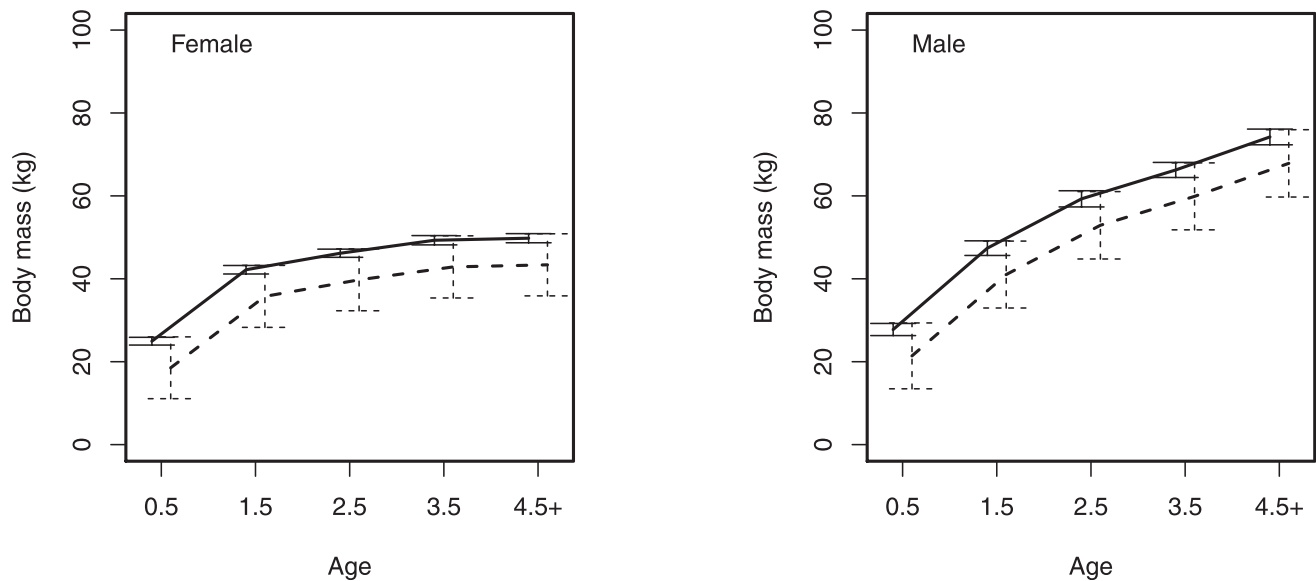


Figure 1. Predicted field-dressed body mass with 95% confidence intervals for female (left, $n = 1,056$) and male (right, $n = 675$) white-tailed deer *Odocoileus virginianus* at mean amount of available cropland (solid line, 19.9% cropland) and management goal of converting 75% of cropland (dashed line, 5.0% cropland) to cool- and warm-season grass at the mean population density (44.3 deer/km²) observed during our study at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2003–2010.

equivalent to an increase in density of 5.5 deer/km² from the mean density of 44.3 deer/km² and a 1-unit decrease in the amount of cropland was equivalent to a decrease in cropland of 3.1% of the total land area from the mean amount of cropland at DNWR (19.9%). We found a positive correlation between amount of available cropland and body mass of all sex and age classes of deer. Females and males of all age classes had a similar response in body mass to amount of cropland (-1.3 kg/3.1% reduction in cropland availability, $SE = 0.8$;

Table 3). The predicted body mass of all sex and age classes was lower for the management goal of 5.0% total land area as cropland when compared with predicted body mass at mean amount of cropland (19.9%) observed during the study; however, 95% CIs overlapped (Figure 1). Change in mass of deer in all sex and age classes was similar and negatively correlated with deer density (-1.4 kg/5.5 deer/km², $SE = 0.8$). The predicted mass of all sex and age classes was lowest, intermediate, and highest for deer at the highest, mean, and lowest

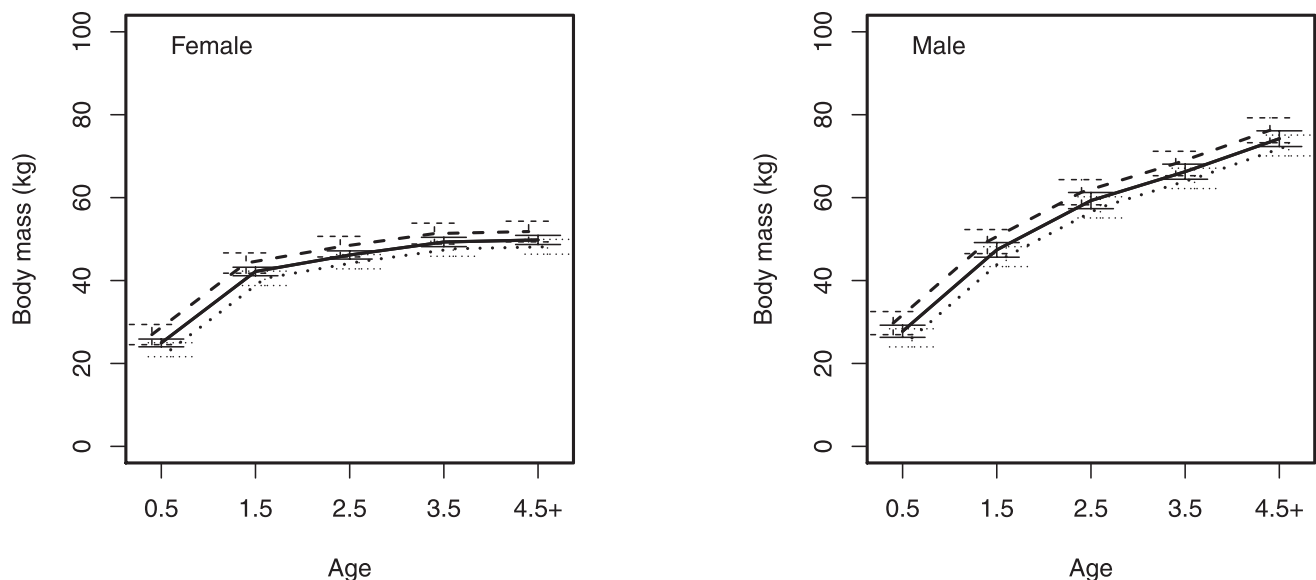


Figure 2. Predicted field-dressed body mass with 95% confidence intervals for female (left, $n = 1,056$) and male (right, $n = 675$) white-tailed deer *Odocoileus virginianus* at highest (dotted line, 50.6 deer/km²), mean (solid line, 44.3 deer/km²), and lowest (dashed line, 36.5 deer/km²) observed densities of deer at the mean amount of available cropland (19.9% cropland) at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2003–2010.

Table 3. Model-averaged parameter estimates and standard errors used to estimate field-dressed body mass of male and female white-tailed deer *Odocoileus virginianus* at DeSoto National Wildlife Refuge in eastern Nebraska and western Iowa, 2003–2010.

Parameter ^{ab}	Estimate	SE
Intercept	24.9	0.5
Male	2.8	0.6
Age 1.5 y	17.2	0.5
Age 2.5 y	21.2	0.5
Age 3.5 y	24.4	0.5
Age ≥4.5 y	24.8	0.5
Density	−1.4	0.8
Crop ^a	1.3	0.8
Male:age 1.5 y	2.4	0.8
Male:age 2.5 y	10.3	1.0
Male:age 3.5 y	14.1	1.0
Male:age ≥4.5 y	21.6	1.0

^a To estimate body mass of a particular sex and age class, add all parameters that are included in the model for the class of interest. For example, body mass of yearling males would include the parameters intercept, male, age 1.5 y, density, crop, and male:age 1.5 y.

^b Density and crop were standardized measures ($\mu = 0$, $SE = 1$). A 1-unit of change in density was equivalent to a change in density of 5.5 deer/km² and 1-unit change in availability of crop was equivalent to a change in cropland of 3.1% of the total land area. Effects of density and crop on body mass are calculated as unit deviations from mean density (44.3 deer/km²) and mean amount of cropland (19.9%) observed during the study.

observed density of deer at DNWR, respectively; however, 95% CIs overlapped (Figure 2). Based on the model estimates, in order to maintain body mass of deer at DNWR, 1.7 deer/km² ($SE = 0.6$) should be removed for every 1% of total land area converted from cropland to cool- or warm-season grassland.

The BCNWR consisted of 0.0% cropland during the study. Hunters harvested 31 and 35 white-tailed deer at BCNWR in 2004 and 2005, respectively. No male deer ≥2.5 y of age were harvested during 2004 or 2005, and no female deer 1.5 y of age were harvested during 2005. Pre-hunt density estimates were 17.7 deer/km² in 2004 and 12.8 deer/km² in 2005. The PIs for mass of deer harvested at DNWR overlapped with mean observed weights at BCNWR (Figure 3). The average difference between predicted and observed deer mass at BCNWR for each sex and age class was −4.2 kg ($SE = 6.9$).

Discussion

Increased harvest rates during our study period were consistent with the management goal of reducing the population of white-tailed deer at DNWR; however, harvest rates were not large enough to result in reduced densities, except during 2006 and 2009. The pre-hunt density estimates used in our predictive models could have underestimated true densities of deer at DNWR because our recruitment-based estimates were always higher than pre-hunt density estimates. Given helicopter surveys were a well-established method and nearly all

deer harvested on DNWR were reported to wildlife law enforcement officers; however, we feel a better explanation of the 10.6 deer/km discrepancy between our density estimates could be attributed to emigration and non-hunting-related mortality. Previous research on white-tailed deer found ~30% of all radiotelemetered deer emigrated from DNWR (VerCauteren 1998; VerCauteren and Hygnstrom 1998; Clements et al. 2011) and 39% of observed mortalities of deer at DNWR were not related to hunting (Frost 2009). Our pre-hunt density estimates (helicopter counts plus counts of harvested deer) most likely provided the most accurate and unbiased estimates of density when compared to our recruitment-based estimates (post-hunt counts plus subsequent year's recruitment) that were prone to multiplicative errors or methods that may not have been robust to a dynamic harvest regime (Beringer et al. 1998; Skalski et al. 2005; Millspaugh et al. 2009).

We assumed the boundaries of DNWR delineated the area where deer foraged, and given results of 20 y of research and the fact our study area was partially surrounded by water, this may be a valid assumption. From 1991 through 2009, deer exhibited high fidelity to their home ranges within DNWR and did not show less fidelity as cropland acres were converted to warm- and cool-season grassland (VerCauteren and Hygnstrom 1998; Walter et al. 2009; Clements et al. 2011). Walter et al. (2009) reported mean overlap of consecutive annual home ranges for individual female deer at DNWR was 77%, regardless of crop availability during 1991–2004. Clements et al. (2011) also found similar home range fidelity (81% overlap) for male white-tailed deer at DNWR from 2004 to 2008. If increased feeding on off-refuge sites compensated for the decrease in the amount of cropland available on DNWR, the effect of cropland would be more difficult to detect and would result in an underestimate of the parameter “crop” and hence, conservative estimates of the influence cropland conversions have on white-tailed deer. Validation of our models with data from BCNWR was a significant test of the capability of our analysis and shows that our models have significant predictive ability and that our estimates of density and cropland were accurate and precise enough to facilitate minimally biased or unbiased parameter estimates.

The four models that accounted for ≥95% of AICc weight of evidence did not contain the most parameters, which would suggest that more complex linear models would not better describe the data. It is likely our top models set had the correct number of influential variables because the highest weighted models contained an intermediate number of parameters (14–18) compared to the range of 5–34 in the entire set of models. The model sex*age+sex*density+sex*crop had an AICc weight of 0.098 and differed from the best model by the addition of two parameters and a $\Delta AICc$ of 3.94. The sex*age+sex*density+sex*crop model, however, contained uninformative interaction effects of density and crop with sex (Table 2; Burnham and Anderson 2002; Arnold 2010). Our top model would have had substantially more weight of evidence had we excluded the

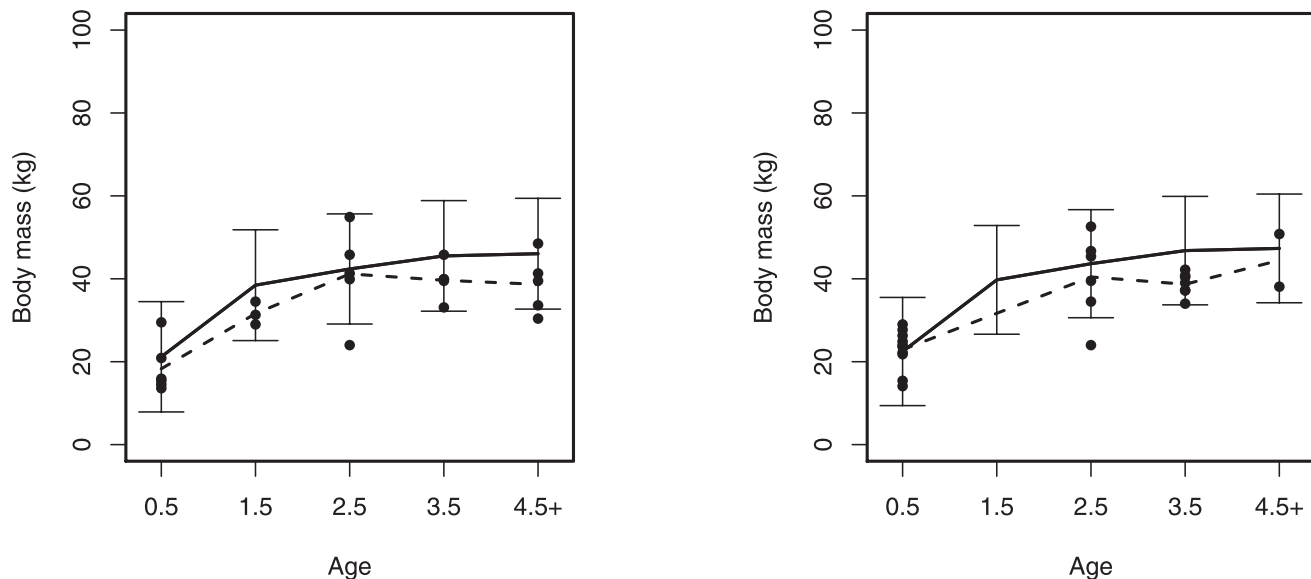


Figure 3. Predicted (solid line) with 95% prediction intervals, mean observed (dashed line) and individual body mass (points) of female white-tailed deer *Odocoileus virginianus* at 0.0% available cropland and observed density of 12.8 deer/km² (left) and 17.7 deer/km² (right) from Boyer Chute National Wildlife Refuge in eastern Nebraska, 2004–2005.

model with uninformative parameters (Arnold 2010). All other models in the >95% of AICc weight set contained fewer parameters and more negative log likelihoods than the best model.

The two hypotheses of most interest, however, were represented by models that had an effect of density and cropland compared to models that did not (the null model and sex*age). We found variables density and crop, however, were collinear ($R^2 = 0.64$), and collinearity had the potential to affect model selection and parameter estimation (Neter et al. 1996; Guthery and Bingham 2007; Smith et al. 2009). Given the high level of collinearity between density and crop and simulation results of Smith et al. (2009), we acknowledge the elevated possibility of a type I error in model selection by concluding an effect of density and crop existed. The possibility of a type I error in model selection, however, seems unlikely given 1) our model-averaging procedures considered uncertainty of parameter estimates due to collinearity of predictor variables, 2) results of our model validation with data collected at BCNWR, and 3) our examinations of parameter estimates within our set of models. Neter et al. (1996) and Guthery and Bingham (2007) reported parameter estimates in models with collinear predictor variables could be biologically nonsensical, highly biased, or have large variance; however, the magnitude of this marginal effect was reported to be highly variable (Neter et al. 1996). To examine the effects of collinearity on our model results, we observed coefficient estimates of models that differed from the top model by the removal of one of the collinear variables. In all combinations, parameter estimates did not vary widely and estimates were what we biologically would expect in that body mass of deer was negatively correlated with density of deer and decreasing amounts of cropland (Guthery and Bingham 2007).

A simple comparison of mean mass for each sex and age class from the two areas showed that deer harvested at BCNWR had lower average body masses than deer at DNWR. Although DNWR and BCNWR were not the same ecosystem, they were only separated by 7 km and were very similar, with the exception that BCNWR had 0% cropland and a lower density of deer and was a smaller area. One or more variables must explain the difference in deer body mass between the two areas because deer were unlikely to be genetically different because mean dispersal distances of deer from DNWR was >7 km (VerCauteren 1998; Clements et al. 2011). Our results suggest that amount of cropland and density likely explain the difference in body mass, and therefore it seems unlikely that we committed a type I error in model selection (i.e., that the model sex*age was in fact the best model) with respect to the variables density and crop given BCNWR validation.

Year and month of harvest may also appear to be important effects as previous research found month harvested influenced observed mass of white-tailed deer (Kie et al. 1983; Mech and McRoberts 1990). We considered these findings and accounted for variation associated with year and month deer were harvested by including a separate random-effect parameter for each year and month combination that deer were harvested. The use of mixed models allowed us to integrate over random variation due to specific sources such as year and date of harvest that otherwise would require a large number of fixed-effects. Mixed models allow users a parsimonious method to quantify the magnitude of the variation of random effects when estimating fixed-effect parameters (Bolker et al. 2009). Additional predictor variables such as precipitation or an index of quality of noncrop vegetation could have been included in our analysis had our objectives been to estimate all

determinants of body mass for deer at DNWR. Our use of a smaller, well-developed model set was consistent with our objectives and the criteria of a confirmatory study (Burnham and Anderson 2002).

Our study corroborated findings of others in that male white-tailed deer were heavier than female deer of the same age class (Roseberry and Klimstra 1975; Kie et al. 1983; Leberg and Smith 1993). Average mass of males and females at DNWR was similar to that reported for deer in another agricultural region of Illinois (Roseberry and Klimstra 1975). Males at DNWR did not reach asymptotic mass until the ≥ 4.5 -y age class, suggesting that an expanded age classification and more accurate method of aging deer might be appropriate to allow for detailed differentiation in mass according to age. Determining age by tooth eruption and wear, however, becomes increasingly difficult with age (Hamlin et al. 2000), so in a post hoc analysis we considered a model (sex+density+crop) that did not consider age classes. Although the model had no scientific support, the parameter estimates of density (-2.3 kg/5.5 deer/km²) and crop (-2.5 kg/3.1% reduction in cropland availability) biologically would be interpreted the same as our model average estimates of -1.4 kg/5.5 deer/km² and -1.3 kg/3.1% reduction in cropland availability, respectively, given the biological interpretation of how many deer should be removed if cropland was converted to grassland was represented by the ratio of the two estimates. Therefore our parameter estimates of density and crop appear robust to errors in age classification if such errors were common and by combining deer ≥ 4.5 y of age into a single class we most accurately represented the limitation of our aging methods and maximized the predictive ability of our models. Future studies, however, may need to incorporate better methods for determining age of deer and additional age classes because high correlation between population density and time needed for males to attain asymptotic mass has been reported (Leberg and Smith 1993).

We expected and found a positive correlation between body mass and amount of available cropland. The fact that male and female white-tailed deer responded similarly to amount of cropland, however, was not expected. Previous research suggested that diets of female white-tailed deer are higher quality than those of males and the sexes demonstrate resource segregation (Beier 1987; Jenks et al. 1994). Female white-tailed deer at the George Reserve, located in Michigan, used grassland habitats and consumed greater quantities of grass than males (Beier 1987; McCullough et al. 1989). The George Reserve, however, lacked cropland so grass may have been the most nutritious forage available in the area during some seasons. In agricultural regions, female deer may consume more agricultural crops than males, which presumably would make female deer more sensitive to changes in amount of cropland. It is not clear whether the magnitude of or percent change in body mass is the correct measure of the effect of diet quality. If we considered the effect of cropland at DNWR by percent change in body mass then females were more sensitive than males to the decrease in cropland availability.

We found an inverse relationship between body mass and density for all sex and age classes of deer, which would indicate densities were high enough to cause a shortage of resources resulting in lower body mass of deer (McCullough 1979). Our results were consistent with other studies that found a density-dependent response in body mass (Kie et al. 1983; Leberg and Smith 1993; Keyser et al. 2005). Keyser et al. (2005) found that body mass was inversely related to 2-y lagged density; however, our results indicate a lagged-density effect was not needed to correlate density with body mass. Testing such an effect would make our results less meaningful to managers and would substantially reduce the amount of data available to estimate parameters. Some studies suggest males were the only group to show a change in mass relative to density or had a greater sensitivity to density (Leberg and Smith 1993; Keyser et al. 2005). We found females were more sensitive to density if the statistic was calculated as a percent change in body mass since all sex and age classes had the same magnitude of response to density.

A physiological maximum and minimum body mass likely exists for white-tailed deer regardless of density of deer or forage availability; however, the shape of the line or curve that connects the maximum and minimum points is unknown. A study in Texas found an average difference in mass of -4.6 kg (-0.6 kg/5.5 deer/km² compared to -1.4 kg/5.5 deer/km² in our study) between white-tailed deer within a predator enclosure at a density of 81 deer/km² and deer outside the enclosure at a density of 40 deer/km² (Kie et al. 1983). Though the authors used a less quantitative analysis than ours, Kie et al. (1983) found the effect of density on body mass of white-tailed deer may be nonlinear, differ by geographical location, or both; however, they didn't consider the effect of forage availability in their study. Based on diagnostics plots, the ranges of density and amount of cropland observed during our study suggest that the shape was linear and extrapolating predictions outside the range of values observed during our study at DNWR may lead to poor predictions and wide confidence intervals (Neter et al. 1996).

None of the 11 sex and age classes of white-tailed deer harvested at BCNWR had a mean weight greater than predicted by our models. Furthermore, deer harvested at BCNWR had a body mass 4.2 kg lower than that predicted from our models on average. Our models were validated in an extreme situation given the amount of cropland at BCNWR was 0.0% during our study and density of the population was about two-fifths that observed at DNWR during the same period. Though we extrapolated our models outside the range of data to predict the body mass of deer at BCNWR, our models performed exceptionally well and PIs appear to capture the variability in the observed data (Figure 3). It is not clear whether density, amount of cropland, small sample size, or a combination of these factors was responsible for lower than predicted body masses observed at BCNWR. At reduced amounts of cropland, however, our results suggest the negative effects reduced cropland availability could be greater than predicted by our models.

Observations prior to our study suggest that as cropland was reduced at BCNWR, body mass of deer deteriorated (S.E. Hygnstrom, University of Nebraska, personal communication); therefore, we suggest that most of the underestimated decline in body mass observed at BCNWR may be attributed to reduction in amount of available cropland. Although severe limitations exist when predicting outside of the range of data used to estimate parameters in a model (Neter et al. 1996), it is useful to note that a reduction in density of about 56% (24.9 deer/km², SE = 9.5) from the average density would be required to offset the negative effects on body mass of reducing the amount of cropland from the current average of 19.9% to the management goal of 5.0% at DNWR. Our conclusion that managers should remove 1.7 deer/km² (SE = 0.4) for every 1% of total land area converted from cropland to cool- or warm-season grassland to maintain body mass of white-tailed deer seems reasonable, although no studies exist for comparison. If all cropland at DNWR was removed (19.9% of available landcover), our model predicts managers would need to reduce densities by 33.2 deer/km² (SE = 12.7) from an average of 44.3 to 11.1 deer/km² in order to maintain body mass of deer.

Management implications

Our study established a direct and linear relationship between mass of white-tailed deer and density of deer and cropland availability (Δ density + Δ proportion of cropland = Δ body mass of deer). Results of model validation indicate our models would have good predictive abilities and could also be used by wildlife managers to estimate the effect that changes in density and land use practices will have on body mass of white-tailed deer. We feel our results can be used by managers as a starting point to an adaptive harvest management scheme to manage populations of deer to maintain body mass and possibly health during times of landcover change in agricultural regions of the Midwest in the United States where habitat conditions are similar to our study areas (Keyser et al. 2006; Koichi et al. 2010). For example, if the management goal is to convert vegetation types from cropland to grassland for biofuel production or other reasons, managers could use the habitat–density relationship identified in our study to estimate the impact the change may have on body mass of deer and could implement harvest strategies to reduce the negative impact. We found that in order to maintain body mass of deer at DNWR or areas with similar habitats, 1.7 deer/km² (SE = 0.6) should be removed for every 1% of the total land area converted from cropland to grassland. Our results indicate population density estimates are not needed for management and that managers can use the desired percent change in cropland and calculate how many deer per square kilometer to remove prior to converting cropland and monitor the body mass to determine if the desired effect occurred. Although the effects of density and cropland have been studied intensely, our study is the only one known to us that can be used directly as a starting point for harvest recommendations if no information about herd condition for the focal population is available.

Supplemental Material

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Data S1. Data for the analysis of white-tailed deer *Odocoileus virginianus* body mass at DeSoto and Boyer Chute National Wildlife Refuge in eastern Nebraska and western Iowa, from 2003–2010 are contained in the Microsoft Excel Worksheet file titled Deer Body Mass Data. Column headings include location and date of harvest, sex, body mass in kilograms, amount of cropland in hectares, and post-harvest abundance estimate.

Found at DOI: <http://dx.doi.org/10.3996/022012-JFWM-015.S1> (82.1 KB XLSX); also archived in Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.hn45t>.

Data S2. Maps detailing helicopter survey efforts and results for white-tailed deer *Odocoileus virginianus* at DeSoto and Boyer Chute National Wildlife Refuge in eastern Nebraska and western Iowa, from 2003 to 2010 are contained in the Adobe Acrobat Document file titled Helicopter Survey Maps.

Found at DOI: <http://dx.doi.org/10.3996/022012-JFWM-015.S2> (608 KB PDF).

Data S3. Maps detailing landcover and cropland at DeSoto and Boyer Chute National Wildlife Refuge in eastern Nebraska and western Iowa, from 2003 to 2010 are contained in the Adobe Acrobat Document file titled Landcover and Cropland Maps. Crop field size is labeled in acres.

Found at DOI: <http://dx.doi.org/10.3996/022012-JFWM-015.S3> (1693 KB PDF).

Reference S1. [FSA] Farm Service Agency. 2010. Conservation reserve program fact sheet. U.S. Department of Agriculture.

Found at DOI: <http://dx.doi.org/10.3996/022012-JFWM-015.S4>; also available at http://www.fsa.usda.gov/Internet/FSA_File/crp_prog_0726.pdf (313.9 KB PDF).

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Deer Body Mass Data. Data for the analysis of white-tailed deer *Odocoileus virginianus* body mass at



DeSoto and Boyer Chute National Wildlife Refuge in eastern Nebraska and western Iowa, from 2003–2010 are contained in the Microsoft Excel Worksheet file titled Deer Body Mass Data. Column headings include location and date of harvest, sex, body mass in kilograms, amount of cropland in hectares, and post-harvest abundance estimate.

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