Journal of Environmental Management 248 (2019) 109299

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Research article

Conservation Reserve Program is a key element for managing white-tailed deer populations at multiple spatial scales

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ARTICLE INFO

Keywords:
Aerial survey
Conservation Reserve Program
Deer management
Habitat selection
North Dakota
Odocoileus virginianus

ABSTRACT

Understanding the underlying mechanisms driving population demographics such as species-habitat relationships and the spatial scale in which these relationships occur is essential for developing optimal management strategies. Here we evaluated how landscape characteristics and winter severity measured at three spatial scales (1 km^2, 9 km^2, and hunting unit) influenced white-tailed deer occurrence and abundance across North Dakota by using 10 years of winter aerial survey data and generalized linear mixed effects models. In general, forest, wetland, and Conservation Reserve Program (CRP) lands were the main drivers of deer occurrence and abundance in most of the spatial scales analyzed. However, the effects of habitat features vary between the home-range scale (9 km^2) and the finer spatial scale (1 km^2; i.e., within home ranges). While escape cover was the main factor driving white-tailed deer occurrence and abundance at broad spatial scales, at a fine spatial scale deer also selected for food (mainly residual winter cropland). With CRP appearing in nearly all top models, here we had strong evidence that this type of program will be fundamental to sustaining populations of white-tailed deer that can meet recreational demands. In addition, land managers should focus on ways to protect other escape covers (e.g., forest and wetland) on a broad spatial scale while encouraging landowners to supply winter resources at finer spatial scales. We therefore suggest a spatial multi-scale approach that involves partnerships among landowners and government agencies for effectively managing white-tailed deer.

1. Introduction

The relationship between animals and their habitats is a foundation of ecology with strong implications for animal conservation and management (Elton, 1927; Leopold, 1933). Limited ecological understanding of species-habitat relationships and species responses to alternative management actions, for example, leads to uncertainty associated with decision making (structural uncertainty; Williams, 1997), which is a recurring management challenge (Bolen and Robinson, 1999; Rupp et al., 2013). In addition, methods currently used to survey wildlife populations are expensive and require specific conditions that are not always met, leading to inconsistent population indices and introducing a second source of uncertainty (partial observability; Williams, 1997). To deal with this, many wildlife agencies are looking at moving forward with an adaptive management approach, a type of structured decision making that allows decision makers to simultaneously manage and learn about natural resources through deliberate iterative processes (Williams, 2011). Population models can assist in this process by identifying optimal strategies under uncertainty; but as part of this framework, understanding the underlying mechanisms driving population demographics such as species-habitat relationships is essential for future management as it provides key information on the managed system.

White-tailed deer is probably the most intensively managed mammal species in North America due to its social and economical value. White-tailed deer populations have increased markedly in the Midwest and eastern half of the United States over the last century (Taber, 1997; Diefenbach and Shea, 2011; VerCauteren and Hygnstrom, 2011). More recently, however, there has been a growing concern by state agencies that after decades of steady increases, deer populations in some areas of the Midwest, such as portions of North Dakota, are now well below management goals (Kreil, 2014; Williams, 2018; WF Jensen, pers. obs.). Generally speaking, white-tailed deer selects for protective cover, including shelterbelts, wetlands, and forest cover (Kramlich, 1985; Whittaker and Lindzey, 2004). Human-related characteristics such as habitat fragmentation and human presence do not seem to be a

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https://doi.org/10.1016/j.jenvman.2019.109299
Received 6 April 2019; Received in revised form 8 July 2019; Accepted 19 July 2019
0301-4797/

major determinant of their habitat use, at least in agricultural landscapes (Roseberry and Woolf, 1998). Previous studies have made predictions about the importance of private lands and the Conservation Reserve Program (CRP) for white-tailed deer (Gould and Jenkins, 1993; Grovenburg et al., 2010b; Grovenburg et al., 2012a, 2012b) but this has not been investigated in a landscape scale yet.

CRP is a land conservation program based on cost-share and rental payment in which farmers are paid to remove highly erodible and environmentally sensitive land from agricultural production and convert them to vegetative cover (FSA/USDA, 2018). The program was initiated in 1985 by the U. S. Department of Agriculture and has the goal to re-establish land cover to help improve water quality, prevent soil erosion, and reduce the loss of wildlife habitats (FSA/USDA, 2018). A report by the U. S. Geological Survey (Allen and Vandever, 2012) compiles hundreds of scientific studies and synthesizes the measureless contributions of CRP in the ecological, social, and economic spheres. Regarding its ecological benefits, CRP increases wildlife abundance, richness, and diversity (Allen and Vandever, 2012). CRP also has positive effects on ungulate populations, providing permanent cover for mule deer (Kamler et al., 2001) and high-quality forage for pronghorn (Griffin, 1991), with a potential to decrease depredation on grains and alfalfa croplands (Griffin, 1991; Sirotank et al., 1991 *apud* Allen and Vandever, 2012). High-priority wildlife for the CRP includes socially or economically valuable species (FSA/USDA, 2018), which includes white-tailed deer.

Here we evaluated how factors measured at varying spatial scales, including the percentage of CRP, influence white-tailed deer occurrence and abundance across a statewide landscape to inform management decision. We hope this will aid managers in identifying critical habitats and conditions needed for long-term sustainability of white-tailed deer populations and the spatial scale at which management should be directed.

2. Methods

2.1. Study area

The North Dakota Game and Fish Department manages white-tailed deer populations primarily through the allocation of harvest licenses across 38 deer hunting units distributed throughout 10 Major Management Units (MMUs) in North Dakota (approx.182,838 km^2), USA (Fig. 1). MMUs were delineated around ecoregions of the state and

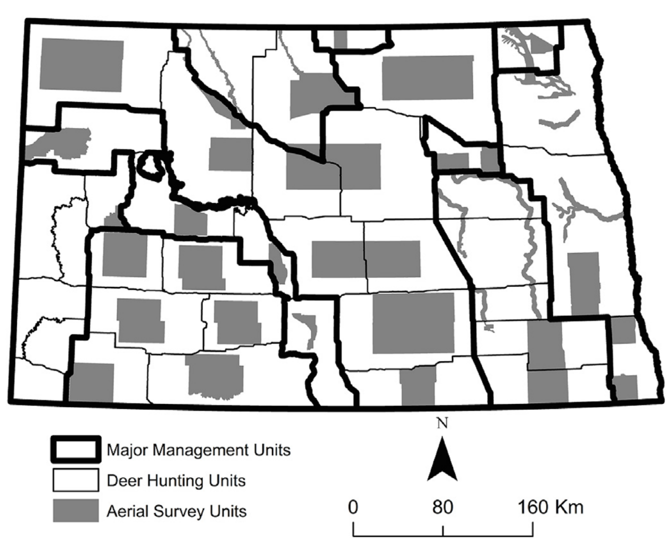

Fig. 1. Location of aerial survey units used to monitor white-tailed deer populations in hunting units and Major Management Units throughout North Dakota, USA.

subdivided into hunting units using major highways as boundaries. The terrain in North Dakota is relatively flat and the climate is cool, sub-humid or semi-arid continental interior, with very cold winters, warm-hot summers, and sparse to moderate rainfall (Seabloom, 2011). Temperatures and precipitation can vary widely. Mean annual temperature ranges from 3 to 6 °C, annual precipitation ranges from 36 to 51 cm, and average total snowfall ranges from 69 to 130 cm (Seabloom, 2011; NOAA, 2018). North Dakota lies within the grassland biome and it holds four main general plant communities: prairie (which extends across nearly the entire state, and encompasses tall-grass prairie, mixed-grass prairie, and short-grass prairie), riparian and upland forests (which also include western conifer stands), wetlands, and badlands (Seabloom, 2011).

2.2. Deer population data

Population minimum counts and locations of white-tailed deer (*Odocoileus virginianus*) were obtained for approximately 10 years from standardized winter aerial surveys (Fig. 1). Surveys consisted of intense searches (census, 100% coverage per unit) from fixed-wing light aircraft at altitudes around 76–107 m and at flight speeds below 130 kph. Winter aerial surveys were made between 1 January and 15 March, when snow depth was sufficient to easily detect deer (> 30 cm; Stillings et al., 2016). All staff were trained to adhere to standardized survey methods and protocol and observers were mostly kept constant throughout data collection. Based on previous sightability trials in our study area – which found that up to 87% of the deer are typically counted by aerial observers (Schaffer, 2013; Sternhagen, 2015) – we assumed sightability bias to be minimal (similar to Christie et al., 2015) and we considered deer minimum counts to be a proxy of deer abundance.

2.3. Spatial scales

We chose three spatial scales for our analyses: one that represents third-order selection (i.e., within home range; Johnson, 1980) for white-tailed deer (1.0 km^2), another that represents second-order selection (9.0 km^2; i.e., location of individual home ranges; Johnson, 1980), and lastly a spatial scale currently used to manage white-tailed deer populations in North Dakota (hunting units). The size of the two smaller scales was chosen based on the winter home range of white-tailed deer in North Dakota (5.2–12.5 km^2; Gullikson, 2019; Seabloom, 2011; Schaffer, 2013; Sternhagen, 2015). We obtained response variables (occurrence and abundance) and covariates for the two smaller spatial scales by superimposing virtual grids of 1.0 km^2 and 9.0 km^2 on the winter aerial survey units and extracting values for each grid cell. For the broader spatial scale, we measured abundance and covariates considering the boundary of each hunting unit.

2.4. Landscape and climate covariates

We assessed which factors influence deer populations by modeling deer occurrence and abundance as a function of landscape characteristics and winter severity. More specifically, our predictor covariates were: areas designated to the Conservation Reserve Program (% CRP), % forest, % grassland (natural grasslands and pastures), % alfalfa (*Medicago sativa*) field, % wetland, % shrubland, % residual winter cropland (primarily fields of corn (*Zea mays*) and sunflower (*Helianthus annuus*), either left standing or harvested, that were planted the previous spring), density of oil/gas wells, and winter severity index of previous year (WSI t-1). These covariates were selected based on their potential to be used in management plans and our current knowledge on deer behaviour and ecology. Land-use information was obtained from the USDA-NASS North Dakota Cropland Data Layers (1:100,000 with a ground resolution of 30 m for most years; USDA-NASS, 2018) and percentage of CRP area was acquired from FSA/USDA. Density of

Table 1
Top models ($\Delta BIC < 2$; cumulative $w_i > 0.8$) used to evaluate the relative importance of factors driving white-tailed deer occurrence and abundance at three spatial scales: third-order selection (1.0 km^2), second-order selection (9.0 km^2), and at hunting unit level (HU).

Spatial Scale	Top Models	BIC	ΔBIC	LL	w_i
OCCURRENCE					
1 km	Occur_WTD ~ CRP + Wetland + Forest + (1|HU) + (1|YEAR)	34996.1	0.0	−17463.1	1.0
9 km	Occur_WTD ~ CRP + Wetland + Forest + (1|HU) + (1|YEAR)	13498.4	0.0	−6720.7	1.0
ABUNDANCE					
1 km	Abund_WTD ~ WSI t-1 + Winter Cropland + (1|HU) + (1|YEAR)	74509.8	0.0	−37196.7	1.0
9 km	Abund_WTD ~ CRP + Wetland + Grassland + (1|HU) + (1|YEAR)	40545.8	0.0	−20220.8	1.0
HU	Abund_WTD ~ CRP + Grassland + Winter Cropland + (1|YEAR)	5870.8	0.4	−2918.8	0.5
	Abund_WTD ~ CRP + Forest + Winter Cropland + (1|YEAR)	5871.8	1.4	−2919.3	0.3
	Abund_WTD ~ CRP + Wetland + Winter Cropland + (1|YEAR)	5872.4	2.0	−2919.6	0.2

oil/gas wells was obtained from the number of oil/gas wells reported by the North Dakota Oil and Gas Division (NDOGD, 2018) divided by area size. Winter severity index of previous year (WSI t-1) was calculated using the number of days with a minimum temperature of -7 °C or lower and the number of days with > 35 cm of snow on the ground. Scores were calculated with 1 point for every day that mean temperature or snow depth exceeded the minimum threshold and 2 points when both conditions exceeded minimum thresholds (Brinkman et al., 2005). Climatic data were obtained from one to three weather stations at each region of North Dakota (north-west, north-central, northeast, west-central, central, east-central, south-west, south-central, and south-east) from NOAA Climatological Data for North Dakota (NOAA, 2018). Climatic data were then interpolated to create a statewide map with WSI estimates. All spatial analyses were performed on ArcGIS software (ESRI, 2009). We standardized (i.e., scaled) all covariates prior to modeling. None of the covariates were highly correlated ($r_s < 0.70$ for all pairs of covariates).

2.5. Modeling procedure

We hypothesized that the landscape and climate covariates affected the occurrence and abundance of deer. To model occurrence, we defined each grid cell as "occupied" (1) if deer were observed within it or undetected (0) otherwise and used a Bernoulli distribution model. To model abundance, we considered the number of deer per grid cell or hunting unit and used a zero-inflated negative binomial distribution for the 1.0- and 9.0-km^2 spatial scales, and a negative binomial distribution for the hunting unit spatial scale. This distribution allows for certain habitats not to be used and does not assume independence in habitat choice across individuals, dealing, therefore, with any problem associated with decisions made by groups rather than individuals. We used the best predictors of occurrence (covariates from the top occurrence models) in the zero-inflated portion of our abundance models and allowed the count portion of the model to vary as a function of covariates.

We used generalized linear mixed-effects models (GLMMs; Bolker, 2008) with random intercepts to account for pseudoreplication while conducting a single analysis for the entire state. Hunting units were considered a random effect for the 1.0- and 9.0-km^2 spatial scale analyses and year was considered to be a crossed random effect for all analyses. Deer counts were adjusted for differential area size by adding this as an offset term to all of our models.

We allowed each parameter to be constant (i.e., null model) or to vary as a function of either a single or a combination of covariates (i.e., additive effect with up to three covariates in each model), modeling all possible combinations as they all represented plausible biological hypotheses. Considering our large sample size (N_{1km} = 174,592 obs.; N_{9km} = 18,606; N_{HU} = 385), we ranked candidate models using Bayesian Information Criterion (BIC), which avoids overfitting models as sample size increases and tends to select the true model when working with large sample sizes (Aho et al., 2014). We considered the covariate(s) from the top-ranked models(s) ($\Delta BIC < 2$) to be the most likely determinant(s) of each deer population parameter at each spatial scale. Additionally, we examined the 95% confidence interval (CIs) of the ß parameters describing the relationships to see if they overlapped with 0 or not (Burnham and Anderson, 2002). Finally, we assessed the predictive ability of our occurrence models using eight-fold cross-validation and estimating the area under the curve (AUC) of our top models (Boyce et al., 2002). For abundance models, we used cross-validation and Spearman's rank correlation coefficient (r_s) between observed and predicted equal-area frequency bins (Boyce et al., 2002; Wiens et al., 2008). In addition, we estimated the marginal and conditional *r*-squared values (r^2) of the hunting unit top model to measure its goodness of fit and its explanatory power. This was not possible for the other spatial scales because they included zero-inflated models. All analyses were conducted in R software (R Development Core Team, 2014) using the packages "glmmTMB" (Magnusson et al., 2018), "pROC" (Robin et al., 2011), "MuMIn" (Bartoń, 2018), and "binr" (Izrailev, 2016).

3. Results

In general, forest, wetland, and CRP lands affected white-tailed deer occurrence and abundance and we did not find any evidence for the effects of the density of oil/gas wells. Nonetheless, deer seem to select a different set of landscape characteristics at each spatial scale (Table 1; Figs. 2 and 3), suggesting that deer occurrence and abundance is highly dependent upon the scale at which relationships are being measured. Top occurrence models had reasonable predictive ability (AUC = 0.7 for all spatial scales). Top abundance models had low predictive ability ($r_s < 0.2$) but good explanatory power and model fit, at least at the hunting unit spatial scale ($r^2 > 0.9$). In addition, models with covariates always performed better than null models, with a difference of $\Delta BIC > 30$ for all spatial scales.

3.1. Management-scale analysis

For the broader spatial scale (i.e., hunting unit), the most important factors determining deer abundance were percentage of CRP, winter cropland, grassland, forest, and wetland (Table 1; Fig. 3). Grassland (natural and pasture) had a negative effect on deer abundance at this spatial scale, and winter cropland had a similar effect albeit not statistically significant (Fig. 3). CRP, forest, and wetland had coefficients that overlapped zero at this spatial scale but they appeared in the top models (Table 1; Fig. 3). We were not able to incorporate shrubland into our hunting unit models due to convergence issues so we cannot infer on its effect at this spatial scale.

3.2. Second-order selection: establishment of home range

Deer selected forest, wetland, and CRP to establish their winter home ranges, as reflected by their role in occurrence models at the 9.0 km^2 spatial scale (Table 1; Fig. 2). These covariates, in addition to

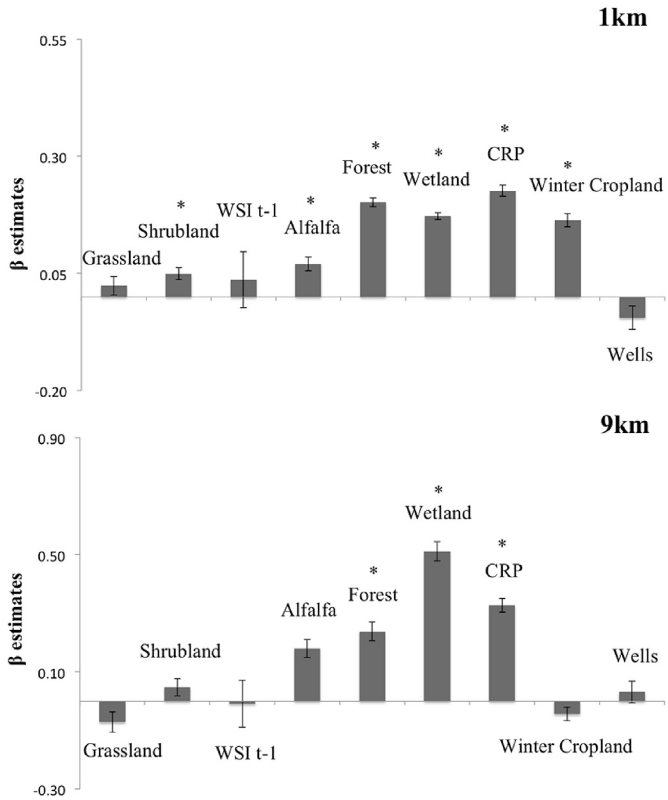

Fig. 2. Influence of landscape and climate covariates on white-tailed deer occurrence at two spatial scales: third-order selection (1.0 km^2) and second-order selection (9.0 km^2) in North Dakota, USA. *Indicates that 95% confidence interval does not include 0.

alfalfa to a lesser degree, also positively influenced deer abundance at this spatial scale, whereas grassland had a negative effect (Table 1; Fig. 3).

3.3. Third-order selection: within home range

In addition to forest, wetland, and CRP, deer likely also select for other habitat features within their winter home range. For instance, the beta estimates describing the relationship between deer occurrence at 1.0 km^2 spatial scale and shrubland, winter cropland, and alfalfa did not overlap with 0, indicating a positive effect on deer occurrence (Fig. 2). As for abundance, we had strong evidence of the positive effect of winter cropland and some positive effect of alfalfa (Table 1; Fig. 3). In addition, winter severity index of previous year (WSI t-1) appeared to have some negative effect on deer abundance at this spatial scale, albeit not statistically significant (Table 1; Fig. 3).

4. Discussion

Ungulates can select landscape characteristics at multiple spatial scales (e.g., Klaver, 2001; Kie et al., 2002; Boyce et al., 2003; Anderson et al., 2005). Here, analyzing white-tailed deer populations across North Dakota, we showed that different landscape characteristics can influence deer occurrence and abundance at multiple scales and that deer-habitat relationships are highly scale dependent. Although some habitat features such as forest, wetland, and CRP appeared to influence deer occurrence and abundance in most of the spatial scales analyzed, the habitat features selected to establish winter home ranges and to move within home ranges were highly dependent on spatial scale. Because different spatial scales had distinct covariates in their top models, we suggest that abundance-habitat relationships at fine spatial scales only weakly matched those found for broad spatial scales.

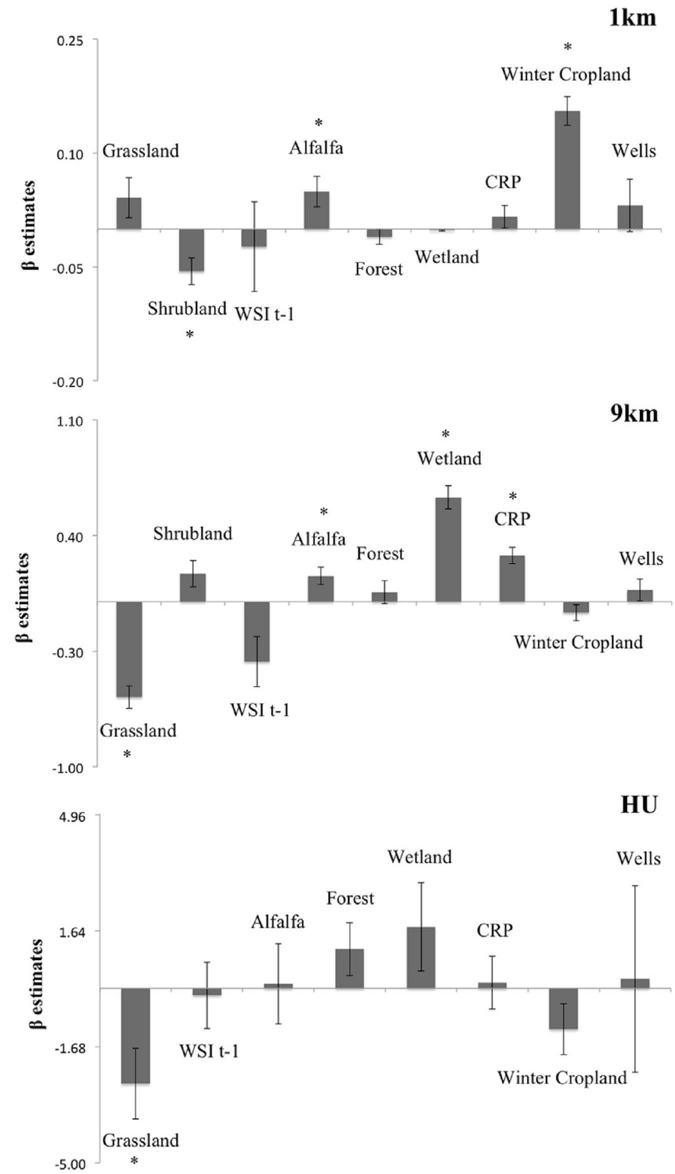

Fig. 3. Influence of landscape and climate covariates on white-tailed deer abundance at three spatial scales: third-order selection (1.0 km^2), second-order selection (9.0 km^2), and at hunting unit level (HU) in North Dakota, USA. *Indicates that 95% confidence interval does not include 0.

Wetland, forest, and CRP were the main factors to be associated with white-tailed deer occurrence at fine and broad spatial scales as well as abundance at the two broader spatial scales (9.0 km^2 scale and at the hunting unit level) during winter. During spring, wetland, forest, and CRP offer forage and escape cover that can be used as bedding site for fawn (Kramlich, 1985; Grovenburg et al., 2010a; Sternhagen, 2015), increasing deer survival and recruitment (Rohm et al., 2007; Sternhagen, 2015; Michel et al., 2018). Because proximity to escape cover influences white-tailed deer vulnerability to predation (Rohm et al., 2007), the use of wetland habitats as hiding cover is a successful antipredator strategy adopted by white-tailed deer (Grovenburg et al., 2012a, 2012b). Similarly, large forest patches can serve as refugia (Rohm et al., 2007), because coyotes (*Canis latrans*), the main deer predator, prefer more open habitats (Seabloom, 2011). Consequently, forest cover can be a critical element for deer distribution (Roseberry and Woolf, 1998), being highly selected habitats in the Dakotas (Gullikson, 2019). During winter, forest cover, especially coniferous stands, minimizes snow depth, acts as a physical barrier against wind, and holds slightly warmer temperatures than open fields, decreasing deer heat loss by offering shelter against adverse climatic conditions (Moen, 1968, 1976). Wetlands also can provide important winter cover for white-tailed deer in the Dakotas (Kramlich, 1985), reducing wind velocity and offering a more favourable microclimate (Schneider, 1985). The higher recruitment in areas with wetland, forest, and CRP during previous spring and the role of these landscape characteristics in deer thermoregulation during winter could help explain their association with deer occurrence and abundance during our winter aerial surveys. Grasslands, on the other hand, provide little winter cover and food, in addition to being the preferred habitats for coyotes in this region (Seabloom, 2011). Not surprisingly, here we found evidence that grassland negatively affected deer abundance during winter at the two broader spatial scales, similar to results from a fine-scale analysis in which white-tailed deer selected against grasslands in South Dakota (Kramlich, 1985).

Relationships for the spatial scale in which management is currently being conducted only slightly aligned with those found at finer spatial scales. While escape cover was the main factor driving white-tailed deer occurrence and abundance during winter at broad spatial scales (9 km^2 and hunting unit level), at a fine spatial scale (i.e., within home ranges, 1 km^2), we saw selection for foods (alfalfa and residual winter cropland of corn and sunflowers). This finding is consistent with the suggested pattern that landscape characteristics at larger scales influence home-range location, whereas food resources are selected at finer spatial scales (Boyce et al., 2003; Boyce, 2006; Gullikson, 2019) and it highlights the importance of a multiple spatial scale approach when investigating ungulate-habitat relationships (also see Kie et al., 2002; Meisingset et al., 2018). In situations such as this where phenomena are scale dependent, inferences about large-scale patterns cannot be made reliably based on small-scale observations (Hobbs, 2003) and landscape features being managed need to be carefully matched with the spatial scale to which the managed population responds. For managing white-tailed deer, we suggest a spatial multi-scale approach: managers should focus their efforts on landscape characteristics related to escape cover at a broader spatial scale such as at hunting unit level, while encouraging landowners to supply food resources (e.g., food plots and cover crops) and escape cover at finer spatial scales.

An interesting result arising from our study is the importance of the Conservation Reserve Program (CRP) for white-tailed deer occurrence and abundance. The most common plants on CRP fields of the Northern Great Plains are grasses, legumes, and annual weeds, but there is a considerable variation among conservation practices (Johnson and Schwartz, 1993). Annual weedy forbs create patches of tall vegetation in some CRP fields of this region (Delisle and Savidge, 1997), which adds more complexity to the landscape; a characteristic that has been found to increases fawn survival on the prairie (Michel et al., 2018). This way, CRP provides important forage and cover for white-tailed deer, and the selection of CRP lands by this species in the Dakotas occurs throughout all seasons (Gould and Jenkins, 1993; Grovenburg et al., 2010b; present study). With intense fragmentation and limited forest cover in North Dakota and other regions of the Northern Great Plains (Smith et al., 2002; Seabloom, 2011), deer might have been forced to seek substitute cover habitats elsewhere, possibly contributing to increased use of CRP areas (Grovenburg et al., 2010b). Also, with ongoing changes in the landscape, we recommend further studies to examine temporal dynamics of deer populations and deer-habitat relationships in the Northern Great Plains.

5. Conclusions

The CRP has greatly enhanced wildlife habitats in the Northern Great Plains, which led to substantial increases in game populations and, consequently, increases in wildlife-based recreation (e.g., hunting; Bangsund et al., 2004). In several areas of North Dakota, for example, the CRP-based hunting revenues override the net economic effect of losses in agricultural revenues, suggesting that CRP is not necessarily an economic burden (Bangsund et al., 2004). With more than 90% of surface area of North Dakota being in private ownership and the ongoing conversion of native habitats to crop production and energy development (Seabloom, 2011), programs such as the CRP will be fundamental to sustaining populations of white-tailed deer that can meet recreational demands. In addition to CRP, land managers should focus on ways to protect the amount of vegetation types that provide other escape covers (e.g., forest and wetland) at a broad spatial scale if the goal is to maintain white-tailed deer populations, which also should help to decrease crop depredation (Kramlich, 1985; Griffin, 1991; Sirotank et al., 1991 *apud* Allen and Vandever, 2012). Considering that private lands contribute to 80% of wildlife habitats in the United States (Benson, 2001), informing the public and policymakers of the value of habitat and CRP on the landscape and working on partnerships among landowners, governments, and communities will be essential to effectively managing wildlife.

Acknowledgment

Financial support for the collection and analysis of these data was provided by the North Dakota Game and Fish Department, United States, Federal Aid Project W-67-R, and the U.S. Department of the Interior, U.S. Fish and Wildlife Service Wildlife Restoration funds, United States, CFDA #15.611. Since 1949, a tremendous amount of effort has been put forth by both pilots and observers to collect winter aerial survey data on white-tailed deer in North Dakota. Since 2004, a total of 22 observers and nine pilots collected the information used in this manuscript. The observers include: A. Anderson, T. Buckley, S. Gaugler, R. Gross, N. Harling, R. Herigstad, R. Huber, P. Isakson, L. Jacobsen, J. Jasmer, W. Jensen, R. Johnson, K. Luttschwager, J. Oster, C. Parent, C. Penner, S. Peterson, D. Repnow, C. Schmitz, J. Smith, B. Stillings, and B. Wiedmann. Pilots include: B. Berentson, J. Blair, B. Debilt, J. Faught, G. Larson, J. Rubbert, R. Rubbert, S. Schneider, and C. Zimmer. Special thanks to C. Penner for assisting with data retrieval. We also thank B. Hosek, H. Pritchert, and C. Wentland who contributed in various aspects to this project. Any mention of trade, products, or firm names is for descriptive purposes only, and does not imply endorsement by the U.S. government. MAL gratefully acknowledges a NSERC Discovery grant and the Canada Research Chair Program. MSB thanks a NSERC Discovery grant and the Alberta Conservation Association.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2019.109299.

Declarations of interest

None.

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