UNDERSTANDING MANAGEMENT AND LANDSCAPE INFLUENCES ON THE HARVEST OF MALE WHITE-TAILED DEER ACROSS A LARGE GEOGRAPHIC REGION

By

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ABSTRACT

UNDERSTANDING MANAGEMENT AND LANDSCAPE INFLUENCES ON THE HARVEST OF MALE WHITE-TAILED DEER ACROSS A LARGE GEOGRAPHIC REGION

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The North American Model of Wildlife Conservation relies on the active participation of citizen hunters to achieve management goals. One factor that motivates hunters to become active participants is an opportunity to harvest a mature white-tailed deer (*Odocoileus virginianus*) with large antlers, especially the case for achievement-oriented wildlife recreationists. Variation in antler conformation and size among white-tailed deer is noticeable across landscapes. Moreover, when mapped, there is obvious spatial heterogeneity in the harvests of record deer (e.g., deer with large antlers that qualify for entry in the Boone and Crockett records) across the United States, with the majority of entries coming from the Midwestern region.

This dissertation should engage the interests of wildlife biologists and researchers. Chapter 1 focuses on testing hypotheses about harvest outcomes for antler point restrictions in the state of Michigan. Chapter 2 evaluates spatially explicit trends in antler sizes of record deer across the Midwestern United States. Chapter 3 evaluates the degree to which management regulations influenced the harvest of record deer in the Midwest United States. Chapter 4 focuses on potential issues related to reporting bias and proposes an adaptation of N-mixture models to account for imperfect detection.

Findings from this research include: 1) the importance of spatial context when evaluating trends in harvest data across a large geographic region; 2) antler point restrictions do indeed protect yearling males from harvest and advance the age structure of male harvest; 3) implementing antler point restrictions did not increase antlerless harvest or change the trajectory

in hunter numbers; 4) antler sizes of record deer in the Midwest showed increasing trends; 5) harvests of record deer were greater in areas with management regulations that restricted the buck harvest; 6) more record deer were reported when at least 1 record deer was reported the previous year; 7) detection of harvests of record deer do not follow any spatial or temporal pattern.

As interest in quality deer management and harvesting adult males with large antlers increases, it is important for wildlife managers and hunters to understand how regulations can influence harvests of record deer. My work offers insights into the relationships between management strategies and harvest outcomes. This research provides managers important information about factors affecting harvests of record deer, outcomes of management regulations, and inherent differences in record deer harvests and characteristics among ecoregions. Managers can draw on the insights gained from this dissertation research during the decision-making process when setting annual hunting regulations, as well as communicating reasonable expectations for deer populations to hunters and other interested stakeholder groups.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

PROLOGUE

This dissertation brought together two of my passions, white-tailed deer and statistics. When I first began working on this research, the focus of the project was to investigate the spatial and temporal distribution in the harvest of white-tailed deer in the Boone and Crockett Club's Records of North American Big Game. Over the years, my dissertation evolved to include 4 distinct chapters, with antlers becoming the common theme. Therefore, I have dedicated most of this prologue to an overview of antlers.

Antlers are secondary sexual characters exclusively found in males of the Cervidae family, except in reindeer where they are seen in both sexes (Landete-Castillejos et al. 2012). Deer grow and shed their antlers every year, requiring large amounts of nutrients and energy (Banks 1974, Ditchkoff et al. 2001), making antlers costly to produce. Antlers grow from the pedicle, which is located on the frontal bone of the skull. Moreover, these secondary sex characteristics constitute one to five percent of the individual's body weight (Landete-Castillejos et al. 2012) and are equivalent to about twenty percent of the animal's skeleton (Grasman and Hellgren 1993).

In general, deer antlers occur in an extensive diversity of sizes and forms, which depend on the individual's age, nutritional consumption, and genetic potential (Strickland and Demarais 2000, Demarais and Strickland 2011). Moreover, other factors such as condition of the mother, date of birth, health of the individual, and weather conditions can affect antler development (Schultz and Johnson 1995, Monteith et al. 2009). Strickland and Demarais (2008) found that antler sizes of white-tailed deer are influenced by landscape composition in Mississippi. Their model suggests a positive influence on antler size in land-use types that promote growth of early successional herbaceous plant communities. Researchers and state agencies use antler measurements to evaluate deer populations because a close relationship between antler size and the nutritional state of the white-tailed deer population exists (McCullough 1982).

Wildlife management agencies typically use a variety of antler characteristics to define the minimum harvest criteria for hunted populations (Strickland et al. 2001). These selective harvest criteria attempt to protect the younger age class to recruit more males into older age classes. However, criteria designed to protect these younger males may have an impact on harvest of the older males (Strickland et al. 2001). Given variability in habitat in which white-tailed deer occur, it is important that harvest criteria be designed based on antler characteristics specific to the population.

In the literature, effects of selective harvesting practices on antler sizes of populations vary. Some studies suggest selective harvesting of yearling males is not likely to influence the genetic potential of antler growth (i.e., low hereditability, Lukefahr and Jacobson 1998, Webb et al. 2012, Hewitt et al. 2014, Webb et al. 2014), usually by citing the complex interactions of environmental factors and various injuries potentially affecting antler development. Other studies suggest that selective harvest at young ages can affect antler size of deer remaining in the cohort at later ages (Strickland et al. 2001, Lockwood et al. 2007, Hewitt et al. 2014, Ramanzin and Sturaro 2014), because of the positive relationship between yearling antler size and antler size at later ages. Allendorf et al. (2008) recommend that managers assume that some genetic change will occur due to selective harvesting and application of basic genetic principles to management strategies for harvested species.

The goal of this dissertation should be to engage interests of wildlife biologists and researchers. The organization of the dissertation is as follows. Chapter 1 uses harvest data of white-tailed deer to investigate harvest outcomes of antler point restrictions in the state of Michigan. This chapter is designed to understand if changes in harvest data are driven by implementation of antler point restrictions. Chapter 2 describes the results of a spatially explicit analysis to investigate trends in antler sizes of white-tailed deer with large antlers. This chapter was inspired by the work of Monteith et al. (2013) that investigated the temporal trends in horn and antler sizes of animals in the book, Records of North American Big Game. Chapter 3 is an investigation into the spatial and temporal distribution in harvests of white-tailed deer with large antlers. The final chapter of this dissertation speaks to potential issues related to reporting bias and proposes an adaptation of N-mixture models (Royle 2004) to account for imperfect detection.

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CHAPTER 1: EVALUATING THE EFFECTIVENESS OF ANTLER POINT RESTRICTIONS TO ACHIEVE WHITE-TAILED DEER MANAGEMENT GOALS

INTRODUCTION

Managers of white-tailed deer (*Odocoileus virginianus*) set hunting regulations based on science and stakeholder input with the intent that harvest outcomes are appropriate for the management goals of an area (Smith and Coggin 1984, Geist et al. 2001, Riley et al. 2002, Hansen 2011, Organ et al. 2012). Fifteen state agencies indicated using some form of antler restriction to help achieve management goals (Quality Deer Management Association [QDMA] Staff 2018). Antler point restrictions are intended to protect younger males from harvest by restricting take to antlered deer with a minimum number of antler points (Carpenter and Gill 1987, Hamilton et al. 1995*a*, Hansen et al. 2017, Wallingford et al. 2017). Support for antler point restrictions is mixed among hunters (Decker et al. 1980, Schroeder et al. 2014) and there have been few tests of the effectiveness of these restrictions in achieving management goals. (Decker et al. 2013, Mason and Rudolph 2015).

Antler point restrictions were first mentioned in the literature by Carpenter and Gill (1987) in their discussion about trade-offs and knowledge gaps associated with these regulations for mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) harvest systems. More recently, alleged costs and benefits of mandatory antler point restrictions have been debated in the popular literature with vocal stakeholders on both sides of the issue (Pinizzotto 2017, YoungeDyke et al. 2017).

In theory, the reduced harvest pressure on yearling males under antler point restrictions will result in higher recruitment of male deer into older age classes (Carpenter and Gill 1987, Hansen et al. 2017, Wallingford et al. 2017). Schroeder et al. (2014) reported that hunters targeting large antlered deer were supportive of antler point restrictions at first, but their support of the regulation decreased over time. The decline in support for the antler point restrictions may reflect unmet expectations that these hunters had for antler point restrictions as a tool for producing large antlered deer (Decker et al. 1980).

Although antler point restrictions are designed to protect the majority of yearling males from being harvested by hunters (Hamilton et al. 1995*a*) and advance the age structure of male deer (Frawley 2012), 2 indirect outcomes of antler point restrictions are also hypothesized. The first is that antler point restrictions will increase the harvest of antlerless deer where implemented. Intuitively, when there is reduced availability of yearling males for harvest, hunters will be more likely to harvest female deer under antler point restrictions (Hamilton et al. 1995*b*, Cornicelli et al. 2011, Hansen et al. 2017, Wallingford et al. 2017, Hansen et al. 2018). The ability to control and stabilize deer populations by increasing antlerless permits or quotas is limited (Curtis et al. 2000, Schroeder et al. 2014), and additional or alternative regulations may add incentives to shift harvest pressure to female deer (Decker and Connelly 1989, Cornicelli et al. 2011).

The second indirect outcome of antler point restrictions is improving hunter recruitment and retention due to increases in perceived opportunities to harvest mature bucks with large antlers (Hansen et al. 2018). White-tailed deer managers rely heavily on active hunter participation to achieve management goals, but declining hunter numbers lead to questions about the effectiveness of hunters in controlling white-tailed deer populations in the future (Brown et al. 2000, Winkler and Warnke 2013). Moreover, an increasing number of hunters are interested in management regulations that could improve their opportunity to harvest mature bucks

(Connelly et al. 2012). However, little is known about the effects of antler point restrictions on hunter recruitment and retention. Therefore, an investigation is warranted because antler point restrictions may influence hunters to move into an area if they perceive that there are more abundant opportunities available.

To date, only a few studies have assessed the harvest outcomes of antler point restrictions in white-tailed deer (Hansen et al. 2017, Wallingford et al. 2017, Hansen et al. 2018), but none have evaluated temporal trends in harvest outcomes leading up to and after antler point restrictions were implemented. Thus, the question remains, do antler point restrictions cause the trajectory of harvest outcomes to change. My objective was to test 3 hypotheses that antler point restrictions caused a change in harvest levels.

H_1 *Male age structure* – Antler point restrictions shift harvest pressure to older aged males

H_2 *Antlerless harvest* – Antler point restrictions increase harvest of antlerless deer

H_3 *Hunter numbers* – The decline in hunter numbers is less severe under antler point restrictions

STUDY AREA

Harvest data from 23 counties in the Northern Lower Peninsula of Michigan offered an ideal case study for investigating how harvest outcomes (male age structure, antlerless harvest, and hunter numbers) changed after implementation of a mandatory antler point restriction because 12 of the counties recently implemented mandatory antler point restrictions (Figure 1.1, Figure 1.2, Frawley 2017). I classified the 23 counties into categories based on regulation history

(Figure 1.1). Since 1991, Michigan hunting regulations have limited hunters to a maximum harvest of 2 antlered deer (i.e., deer with at least one antler measuring ≥7.62 cm). In 1997, Michigan enacted a statewide regulation placing an antler point restriction on the second tag of harvested antlered white-tailed deer. For hunters that harvested 2 bucks per year, the antler point restriction required at least 1 of the bucks harvested to have ≥4 antler points on a side. Moreover, hunters who purchased a single buck tag were not required to follow the antler point restriction, thus any legal antlered deer could be taken. In 2013, mandatory antler point restrictions, which prohibited hunters from harvesting any antlered white-tailed deer with fewer than 3 points on one side, were enacted in 12 counties in the Northwest Lower Peninsula (hereafter referred to as NW12, Figure 1.1) based on a proposal by the Northwest Michigan Chapter of the Quality Deer Management Association (Frawley 2012). One goal of the NW12 antler point restriction was to advance the buck age structure (Frawley 2012). Eleven adjacent counties (referred to as non-antler point restriction [non-APR]) served as a control treatment for comparison (Figure 1.1). Counties of NW12 and non-APR were characterized by similar landscapes (e.g., mostly forested with some agriculture, little residential or commercial development). More importantly, the NW12 and non-APR counties were under similar regulations (e.g., season lengths, weapons permitted, disease controls) with exception that the first buck tag remained unrestricted during the years of the study in the non-APR counties. The similarities between NW12 and non-APR counties allowed for reasonable comparisons of harvest outcomes between the two groups.

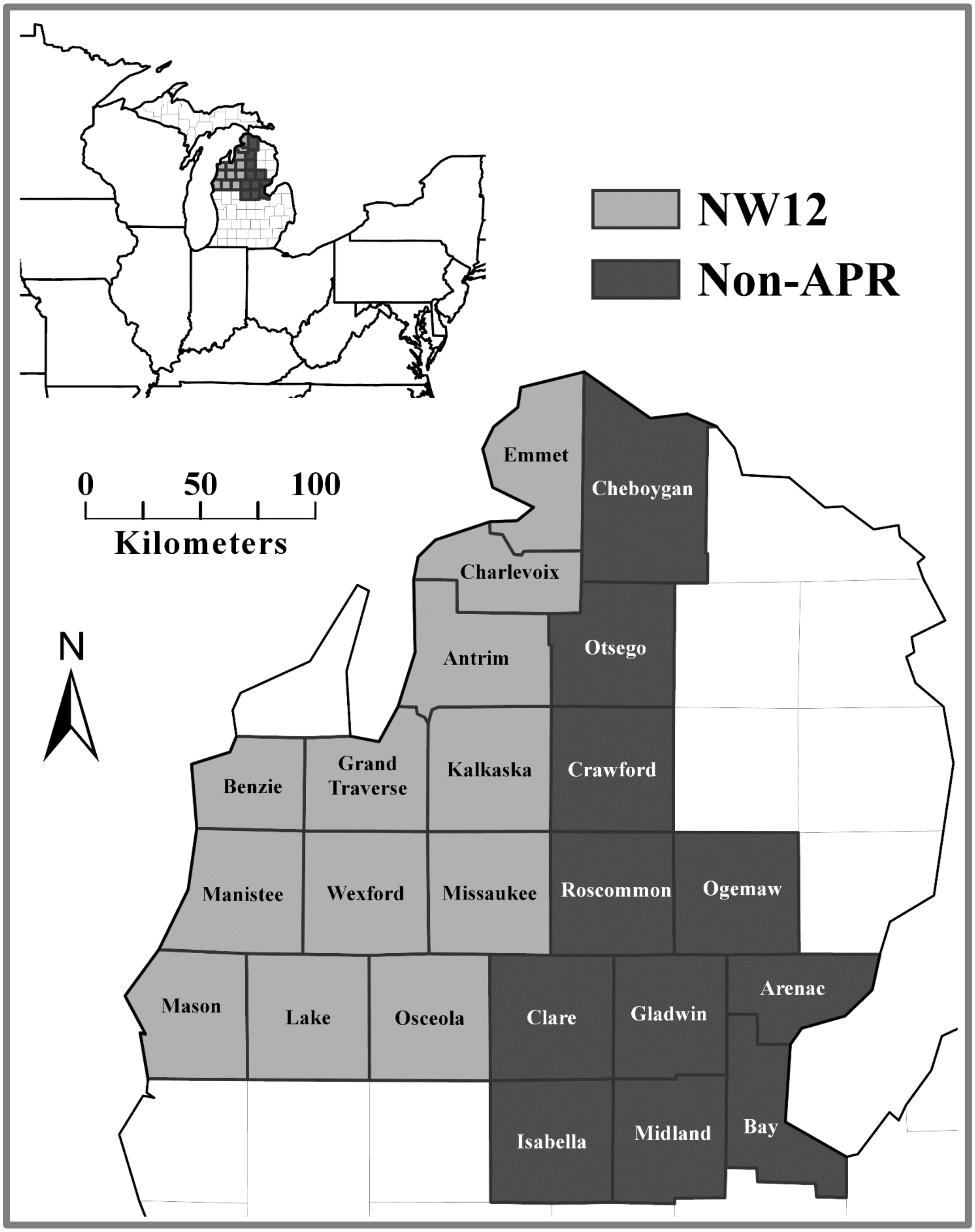

Figure 1.1 Study area for examining how harvest outcomes changed after the implementation of mandatory antler point restrictions. The 23 counties across the northern Lower Peninsula of Michigan were differentiated into categories based on their regulation history. The NW12 counties (light gray) had mandatory antler point restrictions, which prohibited hunters from harvesting any antlered white-tailed deer with fewer than 3 points on one side. The non-APR counties (dark gray) were where the first buck tag remained unrestricted during all the years of the study (1987–2016).

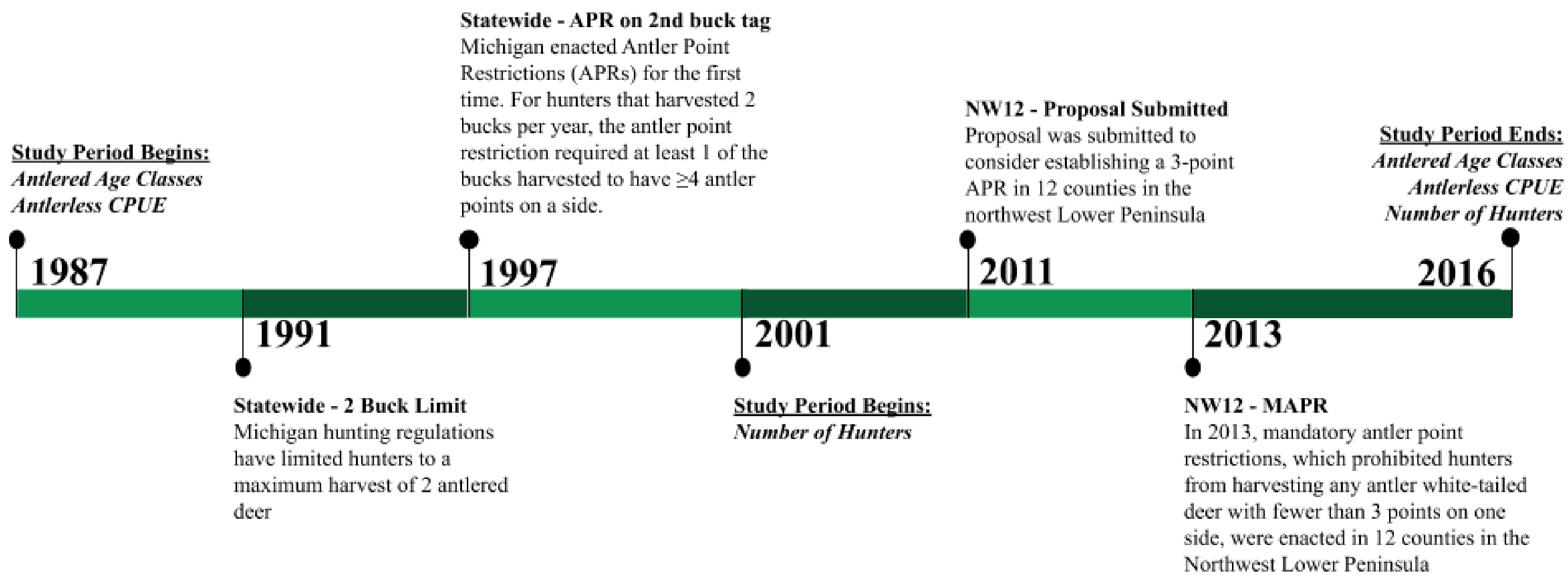

Figure 1.2 Timeline of important events related to deer management regulations in Michigan. This timeline also includes the beginning and ending years of the study period for the analyses in this chapter.

METHODS

Data Collection

I acquired harvest data from 2 sources: deer check-station records (1987–2016) and annual harvest surveys (2001–2016). I used check-station data to obtain information about the age structure of harvested deer and harvest survey data to determine changes in a population index and hunter numbers. For over 50 years, Michigan Department of Natural Resources (MDNR) personnel collected information from hunter-harvested deer at voluntary check stations, including the county in which the deer was harvested as well as the sex and age of the deer. Data from voluntary check stations are used by the state to monitor composition and health of the deer herd (MDNR 2016). MDNR personnel estimated the age of each checked deer using the tooth-wear and replacement technique (Severinghaus 1949), and in cases where the age could not be determined, the deer was categorized as either “not a fawn” or “not a fawn or yearling.” Given my interest in understanding trends in buck age structure, I excluded deer that could not be properly aged (e.g., unable to extract jawbone) from my analyses. For each year and county in the study area, I calculated the proportion of 3 different age classes (e.g., 1.5-year, 2.5-year, and ≥3.5-year classes) in the total male harvest that was reported at voluntary check stations from 1987 to 2016.

I extracted county-level data about estimated number of hunters, hunter effort (i.e., days afield), and harvest of antlerless deer from 2001 to 2016 from the Michigan Department of Natural Resources annual harvest survey reports. These reports are generated from hunter responses to a mailed survey about their deer hunting experience. Given that antler point restrictions may alter hunter effort (Miller and Vaske 2003, Seng et al. 2017), I calculated an antlerless catch per unit effort (CPUE) index by dividing total antlerless harvest by hunter effort for each county in each year. Antlerless catch in this case is synonymous with antlerless harvest. Prior to the 2001 hunting season, the state was divided into 8 regions (Appendix) related to administration units for wildlife management of the Department of Natural Resources (Frawley 2001). Each region spanned multiple counties and harvest data were collected and summarized according to the region where the hunt occurred (Frawley 2001). Consequently, harvest data from the surveys were not available at smaller spatial scales, such as individual counties. To ensure this change in spatial scales did not influence my analysis, I only used harvest data from the annual survey reports for years when county-specific information was available (i.e., 2001–2016).

Statistical Analysis

I used the proportion of 1.5-year, 2.5-year, and ≥3.5-year old male deer in the harvest as response variables to test the hypothesis about influence of antler point restrictions on age structure of the male harvest (H_1). I used antlerless CPUE index to test the hypothesis that antler point restrictions influence antlerless harvest (H_2). Lastly, I used number of hunters from 2001-2016 to test the hypothesis that antler point restrictions influence hunter recruitment and retention where they are implemented (H_3). For each hypothesized harvest outcome, I analyzed county-level data of the response variables, so I had multiple data points for each year.

I used piecewise regressions to investigate the influence of antler point restrictions on different harvest outcomes (Flora 2008, Crawley 2013). For each hypothesis, I analyzed the trend in each response variable (proportion of male age classes, antlerless CPUE, number of hunters) across years. I identified changes through time in longitudinal data by fitting a trend line (or line of best fit) to understand the relationship between my response variable and time (Stasinopoulos and Rigby 1992, Flora 2008). However, the trend may nonlinear through time (e.g., declining trend initially but increasing later), so I tested different breakpoints to identify the year for which the trends before and after were most different (Stasinopoulos and Rigby 1992, Crawley 2013). I identified the breakpoint for each hypothesized trend (Stasinopoulos and Rigby 1992) and calculated the slope and intercept of the trends for the timeframes before and after the breakpoint (Flora 2008, Crawley 2013). Therefore, instead of 1 linear trend through time, which assumes a consistent trend in the response, I created a nonlinear regression model with 2 trends, split at the year where the 2 lines would be most different.

Rather than visually selecting a breakpoint based on a scatter plot of the data, I let the data inform where the breakpoint should occur (Stasinopoulos and Rigby 1992, Crawley 2013). I used a piecewise regression model to identify the year to serve as the optimal break (ψ_j) for the response variables of each hypothesis j. For each response variable, I considered a range of possible years as the optimal breakpoint and compared the deviance values of models with different breakpoints to select the break that fit the data best. I then used the year from the model with the smallest deviance value as the optimal breakpoint (ψ_j). If antler point restrictions influenced the harvest outcome j, I would expect ψ_j = 2013.

Although the piecewise regression models for each hypothesis j had different response variables, they followed the same general format of a 2-segment piecewise regression (Crawley 2013). Data were specified for each county i for

$$(y_i)_j = \begin{cases} \beta_1 x_i + k_1, & x < \psi_j \\ \beta_2 x_i + k_2, & x \geq \psi_j \end{cases},$$

where the relationship between the response (y_i) and year (x_i) is different before and after the break (ψ_j). When $x < \psi_j$, the relationship is linear with slope (β_1) and y-intercept (k_1), whereas when $x \geq \psi_j$, the relationship, while still linear, has a different slope (β_2) and y-intercept (k_2).

Once the breakpoint was identified, I performed an analysis of variance (ANOVA) comparing the 2-trend model with the breakpoint to a null model, which was a simple linear regression with no breakpoint, to determine if the breakpoint model was a significant improvement over the null model (Crawley 2013). If the model with 2-trends did not provide significantly more information than the null model, then only the trend of the null model was interpreted. If the piecewise regression model was a significant improvement over the null model, I determined if the trend was increasing, decreasing, or constant over the years before and after the break by looking at slopes of lines.

I performed the analyses of data from the NW12 counties separately from analyses with data from the non-APR counties. This distinction allowed comparison of the results among the counties had that recently implemented antler point restrictions and counties that had not. I compared slopes of trends between the NW12 and non-APR county groups. I used this comparison to determine if the trends of the NW12 differed from trends in surrounding counties without antler point restriction. If the confidence intervals of the slopes overlapped, I concluded that the slopes between the NW12 and non-APR groups were not different.

RESULTS

Age Structure of Male Harvest

Male deer registered at voluntary check stations among the NW12 counties averaged 214.89 deer/county (SD = 146.39, range: 24–887 deer; n = 77,362 male deer) across all years of this study. The age structure of male harvest varied among counties and across years. From 1987–2016, average proportion of male deer registered at check stations in the 1.5-year age class was 0.60 deer/county (SD = 0.17, range: 0.06–0.84; n = 49,050 yearling males), 2.5-year age class was 0.19 deer/county (SD = 0.08, range: 0.05–0.51; n =13,844 male deer in 2.5-year age class), and ≥3.5-year age class was 0.13 deer/county (SD = 0.11, range: 0.00–0.58; n = 7,650 male deer 3.5-years and older).

Piecewise regression models on the effects of antler point restrictions on age structure of checked male deer fit the data best (i.e., had the smallest deviance value) with a break when $\psi = 2013$ (Figure 1.3, Figure 1.5, Figure 1.7). Moreover, results from the ANOVA comparisons showed that each of the piecewise regression models with the optimal break was an improvement over simple linear regression over the entire timeframe (1.5-year olds: $F = 320.6, p \leq 0.001$; 2.5-year olds: $F = 92.6, p \leq 0.001$; ≥3.5-year olds: $F = 211.5, p \leq 0.001$). There were noticeable changes in the proportion of males harvested in each age class between the 2012 and 2013 hunting seasons. The proportion of 1.5-year old males estimated for the 2013 hunting season was 59.7% less than the estimated harvest of the 2012 season (Figure 1.4). Conversely, there was an 81.3% increase in the proportion of 2.5-year old males (Figure 1.6) and a 120.2% increase in the proportion of ≥3.5-year old males harvested in 2013 than in 2012 (Figure 1.8). During the years after the break, the trend in the harvest of 1.5-year old males was stable (i.e., not increasing or decreasing; $\beta = -0.014, p = 0.179$). The trend in the proportion of 2.5-year olds in male harvest was also stable ($\beta = -0.013, p = 0.052$) over the years following the break, whereas the trend for males in the ≥3.5-year age class increased ($\beta = 0.041, p \leq 0.001$) during the same years.

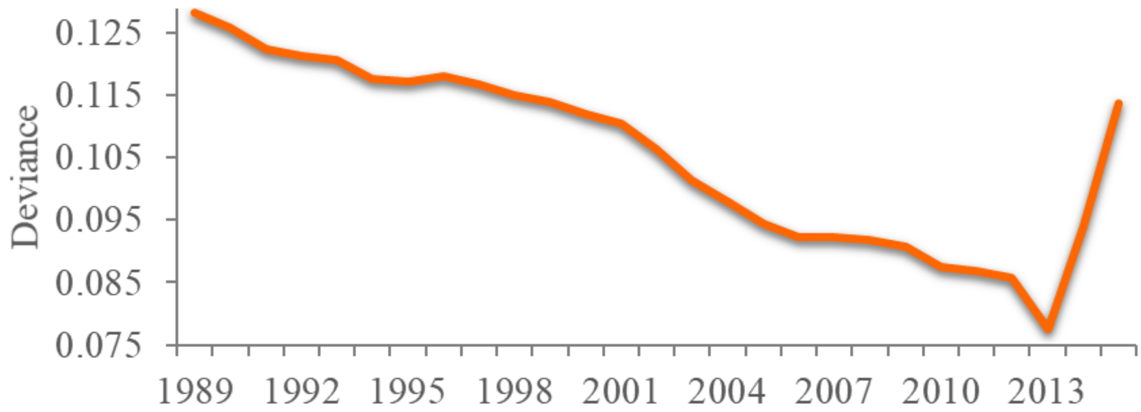

Figure 1.3 Deviance plot for the proportion of 1.5-year old deer in the male harvest (1987–2016) for 12 counties in the northwest Lower Peninsula (NW12) of Michigan. Antler point restrictions were implemented within the NW12 in 2013. Smaller deviance values indicate better fit of trend lines when the breakpoint occurs in that year. This plot shows that the model with the smallest deviance value was with a breakpoint in 2013 ($\text{Deviance}_{\text{min}} = 0.077$).

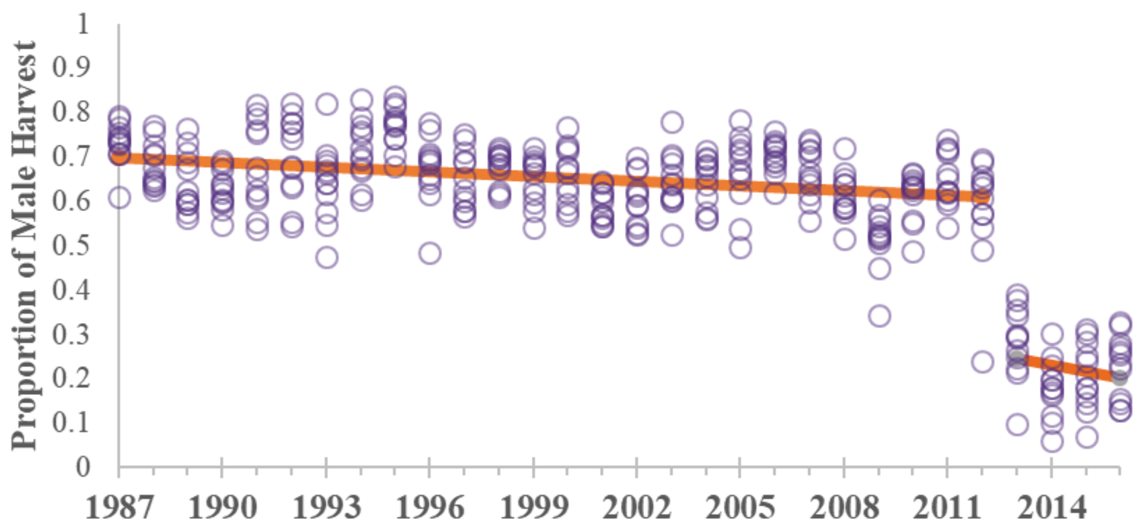

Figure 1.4 Piecewise trends (orange lines) in the proportion of 1.5-year old deer in male harvest from 1987–2016, with a breakpoint in 2013. Open circles (purple) are the calculated proportions for each of the 12 counties in the northwest Lower Peninsula (NW12) of Michigan. Antler point restrictions were implemented within the NW12 in 2013.

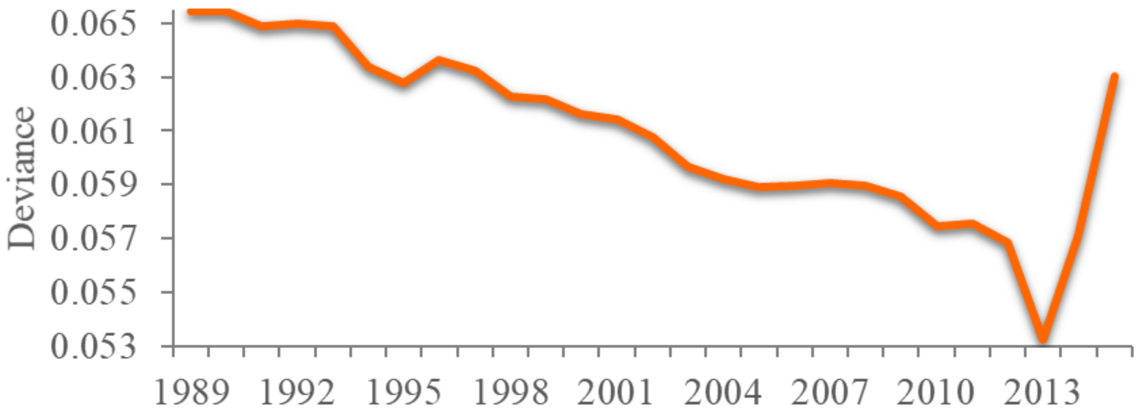

Figure 1.5 Deviance plot for the proportion of 2.5-year old deer in the male harvest (1987–2016) for 12 counties in the northwest Lower Peninsula (NW12) of Michigan. Antler point restrictions were implemented within the NW12 in 2013. Smaller deviance values indicate better fit of trend lines when the breakpoint occurs in that year. This plot shows that the model with the smallest deviance value was with a breakpoint in 2013 ($\text{Deviance}_{\text{min}} = 0.053$).

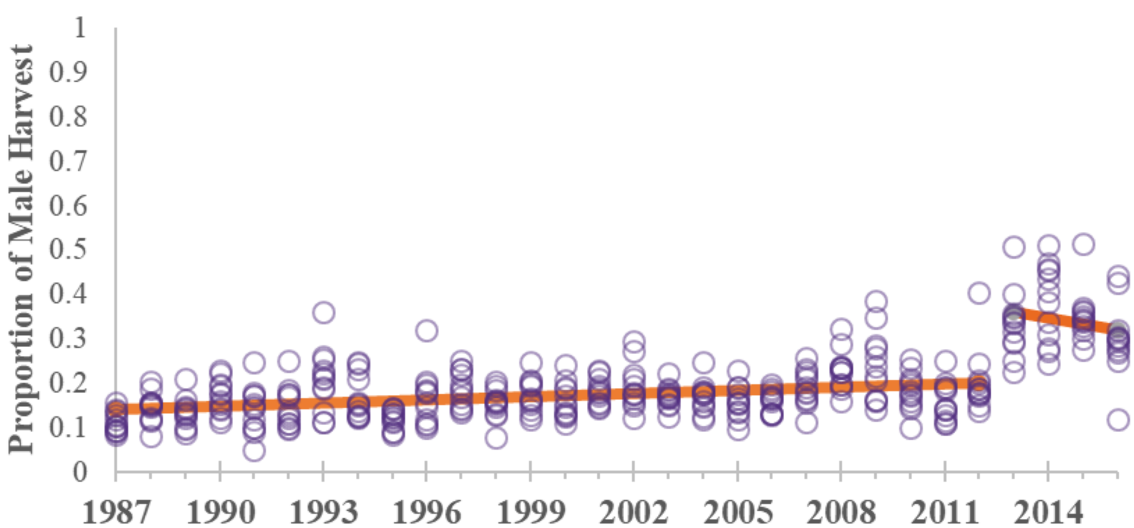

Figure 1.6 Piecewise trends (orange lines) in the proportion of 2.5-year old deer in male harvest from 1987–2016, with a breakpoint in 2013. Open circles (purple) are the calculated proportions for each of the 12 counties in the northwest Lower Peninsula (NW12) of Michigan. Antler point restrictions were implemented within the NW12 in 2013.

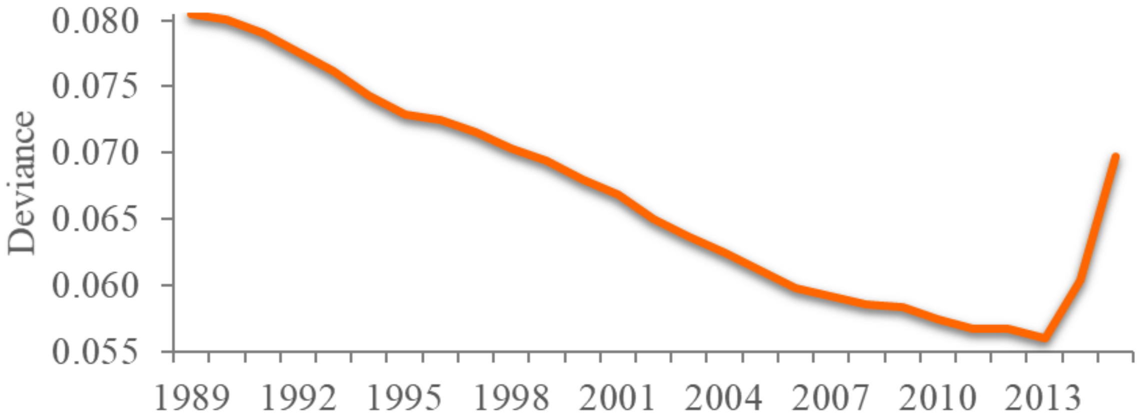

Figure 1.7 Deviance plot for the proportion of ≥3.5-year old deer in the male harvest (1987–2016) for 12 counties in the northwest Lower Peninsula (NW12) of Michigan. Antler point restrictions were implemented within the NW12 in 2013. Smaller deviance values indicate better fit of trend lines when the breakpoint occurs in that year. This plot shows that the model with the smallest deviance value was with a breakpoint in 2013 ($\text{Deviance}_{\text{min}} = 0.055$).

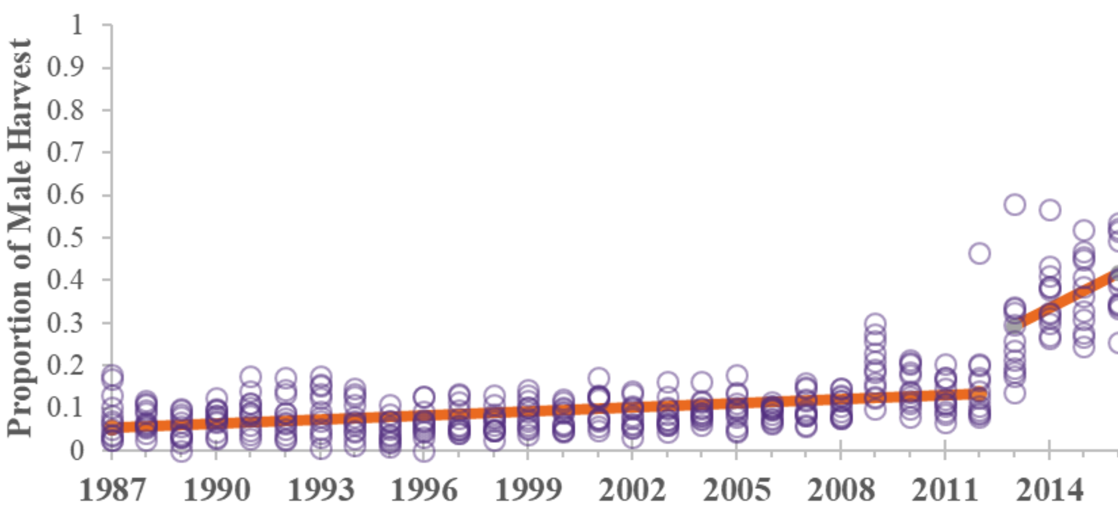

Figure 1.8 Piecewise trends (orange lines) in the proportion of ≥3.5-year old deer in male harvest from 1987–2016, with a breakpoint in 2013. Open circles (purple) are the calculated proportions for each of the 12 counties in the northwest Lower Peninsula (NW12) of Michigan. Antler point restrictions were implemented within the NW12 in 2013.

Antlerless CPUE

From 2001–2016, antlerless harvest in the NW12 averaged 1,712 deer (SD = 1,230; range: 114–6,903; n= 328,767 antlerless deer), whereas antlerless harvest in the surrounding counties where there were no antler-point restrictions averaged 2,279 deer (SD = 1,390; range: 63–5,180; n = 401,277 antlerless deer). Over the same timeframe, hunters in the NW12 spent an average of 98,558 days afield (SD = 37,589; range: 39,301–217,131; n = 18,923,219 days). The average number of days spent afield (119,341 days) was greater in the surrounding counties where there were no antler-point restrictions (SD = 43,106; range: 48,185–207,733; n = 21,004,065 days).

For the NW12, the best fitting model for antlerless catch per unit effort (CPUE) included a breakpoint at $\psi = 2007$ (Figure 1.9). Models that were least supported by the data were those with a break in any year after antler point restrictions were implemented in the NW12 (Figure 1.9). The piecewise regression model was a significant improvement over the null model ($F = 26.7, p \leq 0.001$). The estimated antlerless CPUE was a 56.4% greater in 2007 than it was in 2006 (Figure 1.10). The data for the interval after the breakpoint suggested a positive relationship between antlerless catch per unit effort and year ($\beta = 0.001, p = 0.01$).

For the non-APR counties, the best fitting model for antlerless CPUE was with a breakpoint in the year 2005 (Figure 1.11). The antlerless CPUE model showed a break in 2005 and was significantly different from the null model for data from the group of non-APR counties ($F = 3.59, p = 0.03$). The trend in antlerless CPUE was stable over the years following the break ($\beta = 0.0002, p = 0.255$, Figure 1.12).

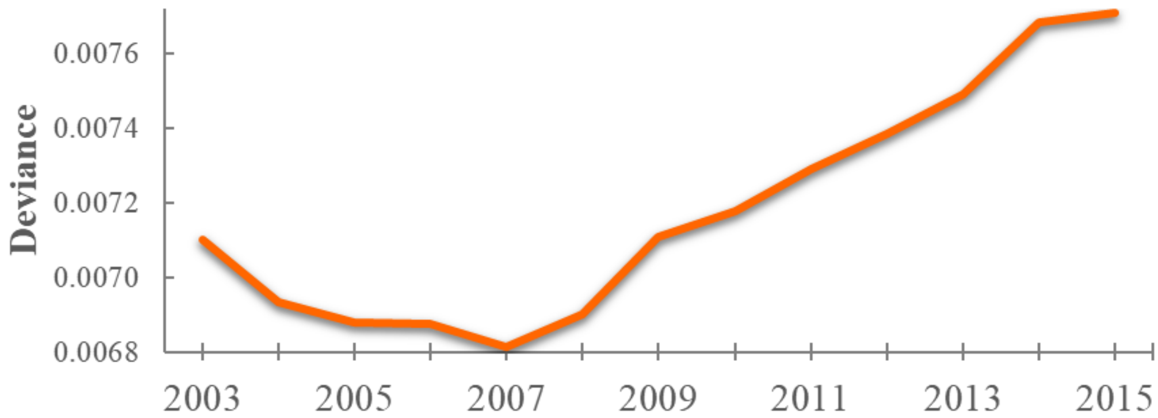

Figure 1.9 Deviance plot for antlerless CPUE (2001–2016) for 12 counties in the northwest Lower Peninsula (NW12) of Michigan. Antler point restrictions were implemented within the NW12 in 2013. Smaller deviance values indicate better fit of trend lines when the breakpoint occurs in that year. This plot shows that the model with the smallest deviance value was with a breakpoint in 2007 ($Deviance_{min}$ = 0.0068).

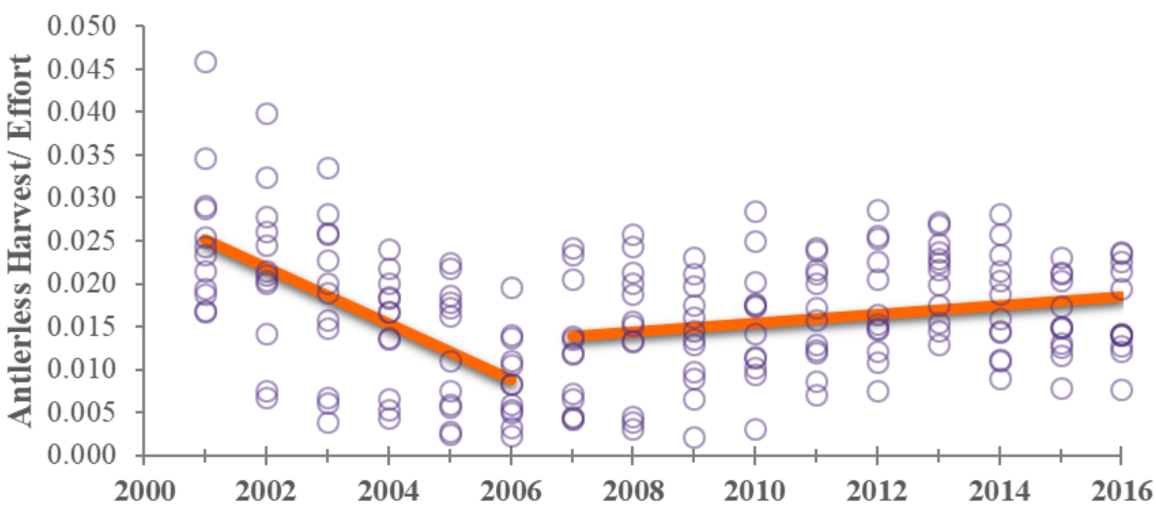

Figure 1.10 Piecewise trends (orange lines) in antlerless CPUE from 2001-2016, with a breakpoint in 2007. Open circles (purple) are the calculated CPUE for each of the 12 counties in the northwest Lower Peninsula (NW12) of Michigan. Antler point restrictions were implemented within the NW12 in 2013.

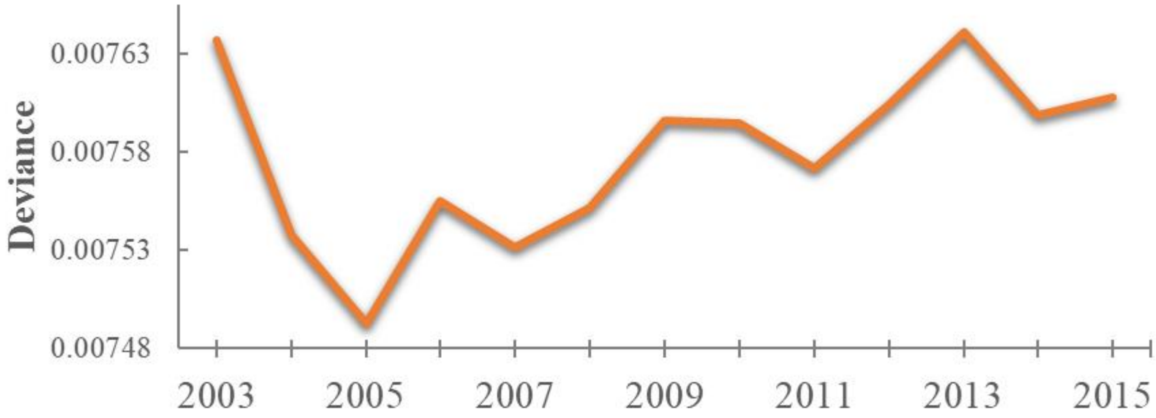

Figure 1.11 Deviance plot for antlerless CPUE (2001–2016) for 11 counties in the northern Lower Peninsula (non-APR) of Michigan. Antler point restrictions were never implemented in these counties over the course of my study. Smaller deviance values indicate better fit of trend lines when the breakpoint occurs in that year. This plot shows that the model with the smallest deviance value was with a breakpoint in 2005 ($\text{Deviance}_{\text{min}} = 0.0068$).

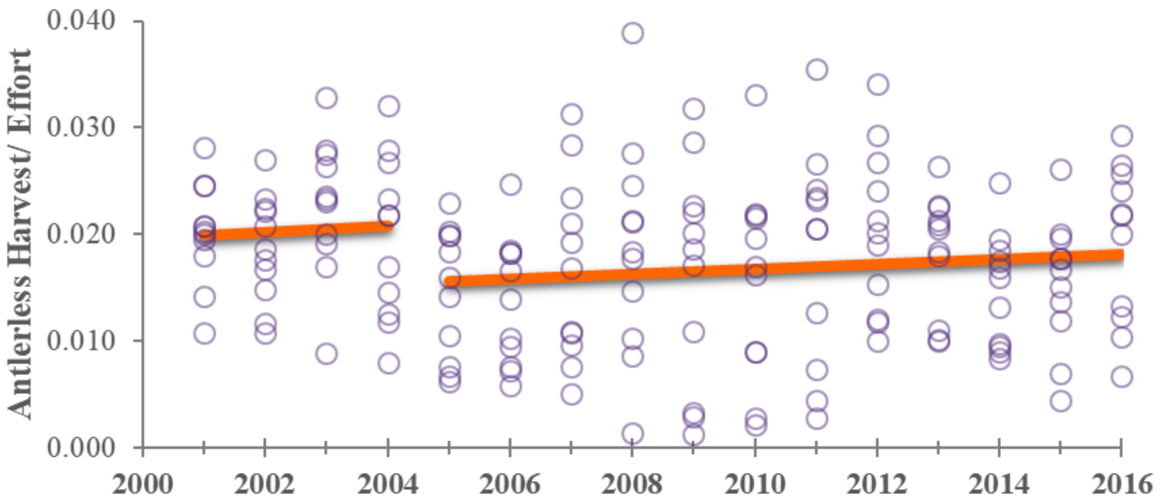

Figure 1.12 Piecewise trends (orange lines) in antlerless CPUE from 2001-2016, with a breakpoint in 2005. Open circles (purple) are the calculated CPUE for each of the 11 counties in the northern Lower Peninsula (non-APR) of Michigan. Antler point restrictions were never implemented in these counties over the course of my study.

Hunter Numbers

From 2001–2016, the number of hunters averaged 9,700 hunters (SD = 4,085; range: 4,372–24,288) in the NW12, whereas hunter numbers in the surrounding counties that have not implemented antler point restrictions averaged 10,885 hunters (SD = 3,882; range: 2,167–19,410).

The piecewise regression model for number of hunters that fit the NW12 data the best included a breakpoint in the year 2005 (Figure 1.13), whereas a break in 2007 was the optimal breakpoint for data from the non-antler point restriction counties (Figure 1.15). However, the piecewise regression models with 2-trends did not provide significantly more information than the null model (i.e., simple linear regression) for the same data (NW12: $F = 2.19, p = 0.11$; non-APR: $F = 0.89, p = 0.41$). Therefore, the null model was used to interpret trends in the number of hunters. The number of hunters in NW12 and non-antler point restriction counties decreased since 2001 (Figure 1.14, Figure 1.16). Furthermore, overlapping confidence intervals of the slopes suggest the rate of decline in hunter numbers was not statistically different between the NW12 ($\beta = -207.65, \mathrm{SE} = \pm 62.33, p = 0.001$) and non-antler point restriction counties ($\beta = -216.77,\ \mathrm{SE} = \pm 61.51, p \leq 0.001$).

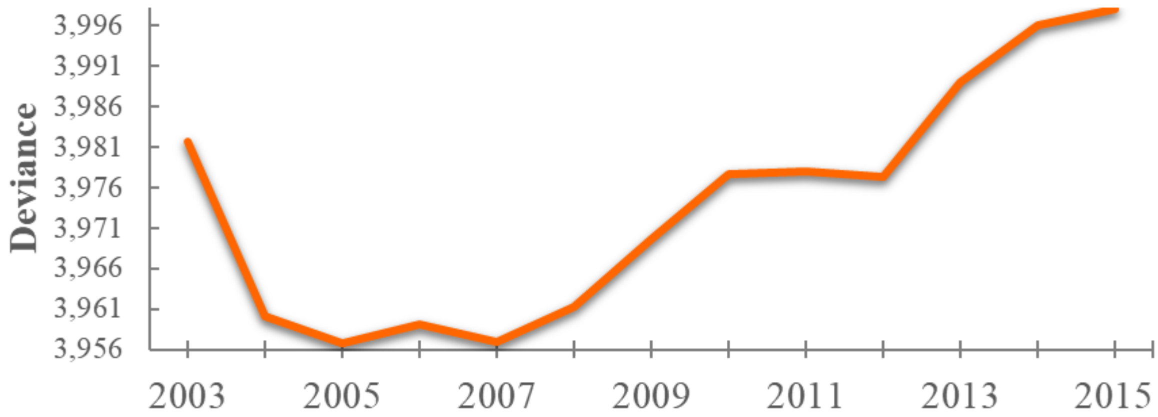

Figure 1.13 Deviance plot for number of hunters in the NW12 counties from 2001-2016. Smaller deviance values indicate better fit of trend lines when the breakpoint occurs in that year. The NW12 is the 12-county area in the northwest Lower Peninsula of Michigan where antler point restrictions were implemented in 2013. This plot shows that the model with the smallest deviance value was with a breakpoint in 2005 (Deviance_{min} = 3956).

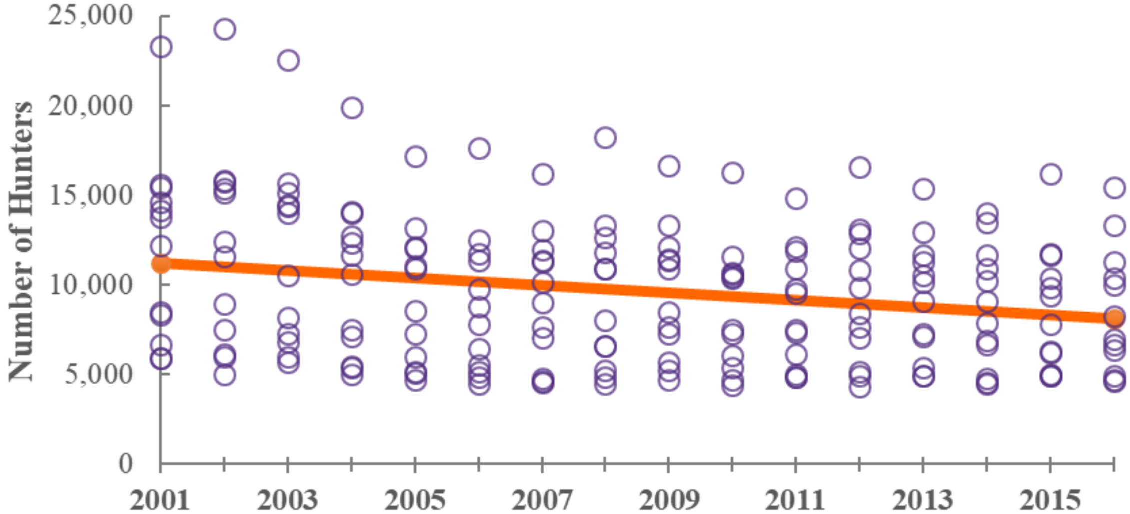

Figure 1.14 Trend (orange line) of the number of hunters in the NW12 counties from 2001-2016. Open circles (purple) are the total number of hunters for each county in the NW12. The NW12 is the 12-county area in the northwest Lower Peninsula of Michigan where antler point restrictions were implemented in 2013.

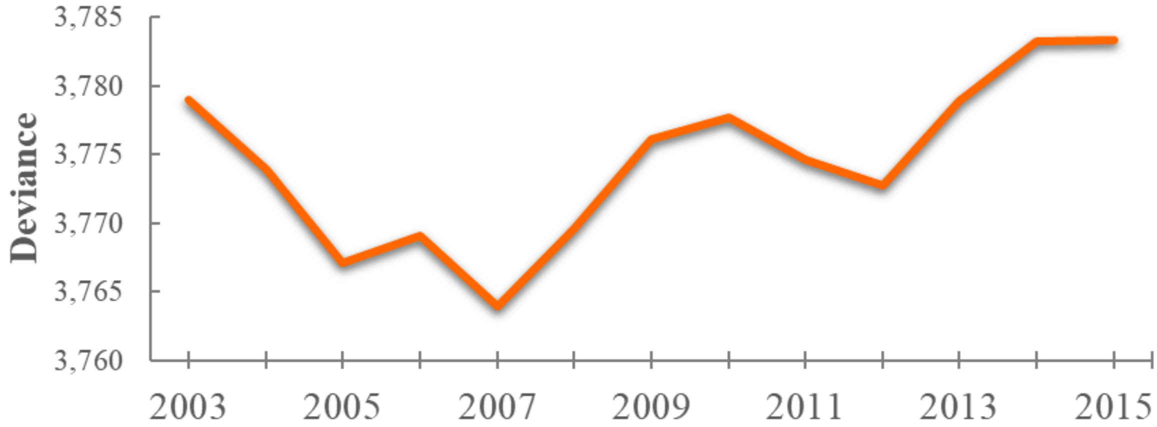

Figure 1.15 Deviance plot for hunter numbers (2001–2016) for 11 counties in the northern Lower Peninsula (non-APR) of Michigan. Antler point restrictions were never implemented in these counties over the course of my study. Smaller deviance values indicate better fit of trend lines when the breakpoint occurs in that year. This plot shows that the model with the smallest deviance value was with a breakpoint in 2007 ($\text{Deviance}_{\text{min}} = 3764$).

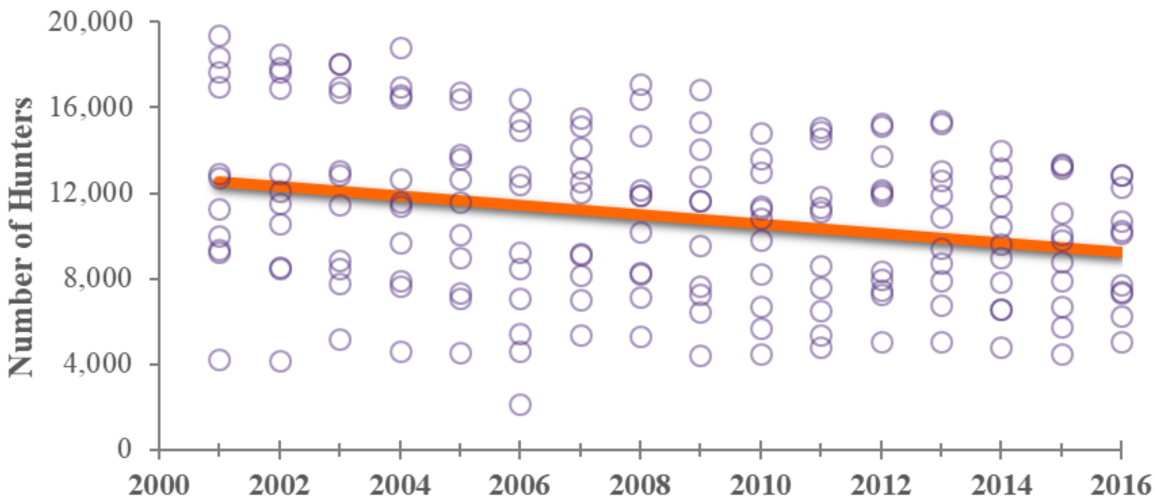

Figure 1.16 Trend (orange line) of the number of hunters in the non-antler point restriction counties from 2001-2016. Open circles (purple) are the total number of hunters for each of the 11 counties in the northern Lower Peninsula (non-APR) of Michigan. Antler point restrictions were never implemented in these counties over the course of my study.

DISCUSSION

The increased proportion of older male deer harvested starting in 2013 suggests that mandatory antler point restrictions implemented in the NW12 increased the age structure of bucks harvested in that area. I found no evidence that antler point restrictions changed antlerless deer harvest or the number of hunters. My analytical approach differs from most analyses looking at outcomes after regulation changes. In general, evaluations compare the means between 2 timeframes (i.e., mean before event, mean after event). Although these comparisons can be useful, this approach assumes that any differences between the means were caused by the regulation change. Conversely, the piecewise regressions used in this paper do not assume that the new regulation caused changes in harvest. Rather, my piecewise regression approach tests this assumption by evaluating trends in the data for the entire timeframe. This ensures that I did not falsely attribute a change in my harvest variables to the new mandatory antler point restrictions.

My finding that antler point restrictions successfully advanced the age structure of harvested male deer differs from harvest outcomes under antler point restrictions on elk (*Cervus canadensis*) and mule deer (*Odocoileus hemionus*) populations in the western USA (Hansen 2011). The regulation in western USA was successful in protecting male deer and elk for 1 year, but these animals generally did not survive the following hunting season (Weigand and Mackie 1987, Biederbeck et al. 2001). If harvest pressure was a major barrier for advancing that age structure of deer and elk in western states, then how can harvest pressure not be an issue in recruitment of older-aged bucks for NW12 populations? One reason is that western hunters, for the most part, are unable to harvest female deer and elk (Hansen 2011). Therefore, hunters in the NW12, in having the opportunity to harvest antlerless deer, are not limited to harvesting only legal males. I hypothesize that the additional harvest opportunities available to NW12 hunters potentially reduce the intensity of hunting pressure on legal males thereby allowing recruitment of older-aged bucks.

Selective-harvest criteria, like antler point restrictions that are designed to protect young males have consequences for harvest of older males (Strickland et al. 2001). A concern of employing antler point restrictions is that male deer will only live one additional year and not survive to older ages because hunting pressure will be high on the 2.5-year age class (Carpenter and Gill 1987). My findings showed an increasing trend in harvest of 3.5-year and older males (Figure 1.8) despite an expected increase in harvest pressure on older males when antler point regulations are in place. Investigations from other states have reported similar increases in the harvest of older male deer (Hansen et al. 2017, Wallingford et al. 2017, Gulsby et al. 2019). Although antler point restrictions are intended only to influence survival of yearling males, there is evidence that harvest vulnerability may decrease with age (Ditchkoff et al. 2001). Therefore, in protecting yearling males, antler point restrictions may indirectly enhance the survival of male deer in older age classes.

I did not find evidence to support the hypothesis that antler point restrictions caused a change in the antlerless harvest. If antler point restrictions influenced my index of antlerless harvest, we would expect the optimal break in 2013. However, my results suggest a positive trajectory in antlerless harvest since the abrupt change in 2007 (Figure 1.9). Therefore, the trend in antlerless harvest after antler point restrictions is actually a consequence of something that occurred around 2007, rather than an outcome of implementing antler point restrictions. The increase in antlerless harvest in 2007 may reflect increases in hunter cooperatives practicing quality deer management (Hamilton et al. 1995*b*), increased hunter willingness to harvest antlerless deer (Adams and Hamilton 2011, deCalesta 2012), or some combined influence of these actions.

The theory underlying the antlerless harvest hypothesis is that if hunters are unable to harvest yearling males due to implementation of an antler point restriction, hunters will focus their harvest on the female segment of the deer population (Hansen et al. 2018). Previous studies suggested that antler point restrictions do not reduce opportunities for hunters to hunt antlerless deer (Wallingford 2012), and there is evidence that hunters may shift their focus, at least in part, to harvesting antlerless deer under these regulations (Hansen et al. 2017). In the NW12, an increase in antlerless harvest occurred during the first year of antler point restrictions but this change was not held through time. Antlerless CPUE in NW12 showed a 15.69% increase from 2012 to 2013, which supports the hypothesis that hunters will harvest more deer that are antlerless under an antler point restriction. However, this increase in antlerless harvest was followed by a 15.17% decrease from 2013 to 2014, so fewer antlerless deer were harvested during second year under antler point restrictions than were harvested before the regulation was implemented. The temporary increase in antlerless harvest during the first year of antler point restrictions aligns with previous suggestions these regulations are a short-term solution for skewed deer populations (Gulsby et al. 2019). In Missouri, hunters perceived that adult males were available in greater numbers under antler point restrictions (Hansen et al. 2018). Therefore, I hypothesize that the decrease in antlerless harvest during the second year is due to changes in hunter perceptions of the availability of adult males that re-shifts hunter focus back to bucks.

Antler point restrictions may show different harvest outcomes for deer populations from differing habitats, even within the same state (Hansen et al. 2017). Hansen et al. (2017) reported that antler point restrictions in Missouri did not increase harvest of female deer in an area of poorer quality habitat, but there was an increase in antlerless harvest in an area of better quality habitat. Habitat quality influenced deer population density and the percentage of 1.5- and 2.5-year old males that could be legally harvested, with inferior habitat having a lower population density and lower percentage of younger males attaining legal status. Deer in the NW12 are impacted by severe winters but have been relatively stable in recent years (MDNR 2019). My findings that antler point restrictions had no influence on antlerless harvest and the contrasting results from 2 different habitats in Missouri speak to the importance of developing restrictions specific to the characteristics of the deer herd that will be affected (Hamilton et al. 1995*a*, Hamilton et al. 1995*b*, Strickland et al. 2001, QDMA Staff 2018).

My results indicated that the number of hunters in the NW12 declined at rates similar to the 11 non-APR counties (Figure 1.14, Figure 1.16). Thus, there was no evidence for a significant change in the number of hunters during the years of this analysis, regardless of whether antler point restrictions were implemented. It is interesting to note that this decline occurred despite survey findings that hunters would hunt the same amount or more often under antler point restrictions, if Michigan DNR implemented them where they hunt (Seng et al. 2017). This discrepancy is consistent with Stedman et al. (2004) that found actual hunter behavior in the field might differ from what has been reported in survey responses. Although regulations can constrain hunter participation (Miller and Vaske 2003), the majority of hunters (about 77%) in the NW12 supported the mandatory antler point restriction (Frawley 2017). Moreover, when asked what could be done to get participants to hunt more frequently, several respondents suggested that the Michigan Department of Natural Resources increase the number of mature bucks and improve herd health; expanding antler point restrictions was mentioned specifically (Seng et al. 2017). Hunters also exhibit high-site fidelity (Cornicelli et al. 2011), which could help explain why hunter numbers did not change in the NW12 relative to non-APR counties. Thus, despite support of antler point restrictions indicated by hunters via survey results, attitudes of hunters toward these regulations were not sufficiently positive to influence hunter movements into the area.

My results suggest that additional harvest regulations, beyond antler point restrictions, are necessary to decrease the size of a deer population. Alternative harvest opportunities must be available (e.g., antlerless tags) for the possibility that hunters shift harvest pressure to antlerless deer when antler point restrictions reduce the availability of harvestable yearling males (Hansen et al. 2017). Hunting participation may inadvertently decrease if implementing these regulation is perceived by constituents to decrease available harvest opportunities (Fulton and Manfredo 2004), especially for those hunting regulations with competing interests (Decker et al. 2015, Hansen et al. 2017). Enhancements to the quality of the deer herd increases hunter satisfaction, specifically satisfactions related to achievement (Elbeling-Schuld and Darimont 2017).

In this chapter, I tested hypotheses related to how deer harvest outcomes change after implementation of antler point restrictions. My findings are of particular importance to deer managers because they often seek to achieve multiple objectives with harvest regulations (Robinson et al. 2019, Fuller et al. 2020). Moreover, there is a growing interest among hunters for regulations designed to produce more mature bucks (Ozoga et al. 1995, Cornicelli and Grund 2011, Connelly et al. 2012, Harper et al. 2012). Thus, if antler point restrictions help achieve multiple management objectives, they would be an excellent tool for managers. Based on the results from this chapter, I conclude that antler point restrictions would be a useful tool where the management goal is to advance the age structure of the male segment of the white-tailed deer herd. However, my results also indicated that antler point restrictions alone would not achieve management goals relating to increasing antlerless harvest or improving hunter recruitment and retention. Although, the arguments for antler point restrictions influencing population growth rate and hunter interest have foundations in logic, I was unable to find definitive empirical support to substantiate these claims.

APPENDIX

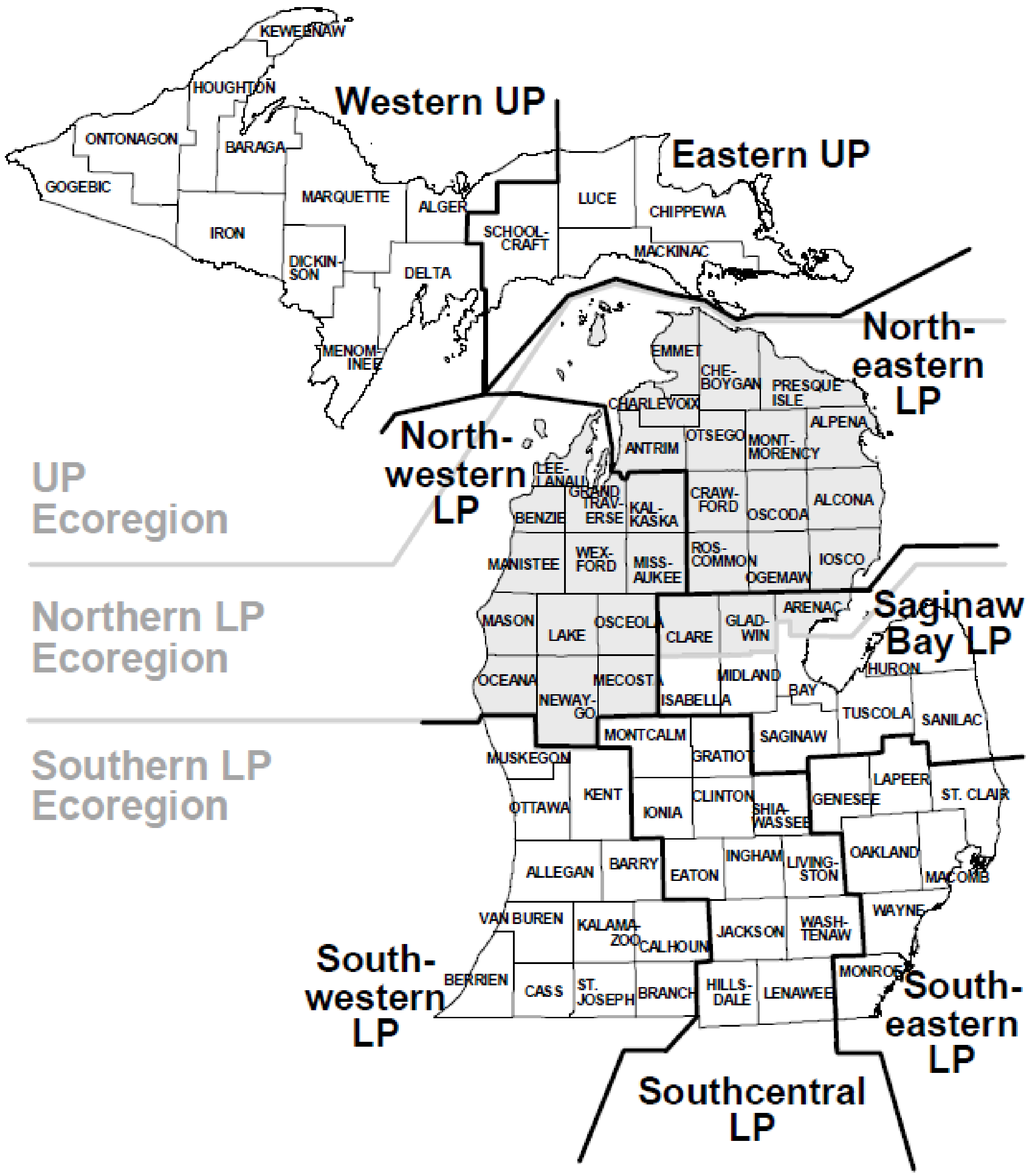

Figure 1.17 A Map of the areas the Michigan Department of Natural Resources (MDNR) used to summarize deer harvest data in the state for the annual hunting seasons. The figure was copied from the Michigan Deer Harvest Survey Report for the Hunting Seasons in 2000 (MDNR Wildlife Report No. 3344, Frawley 2001).

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CHAPTER 2: ANTLER SIZES IN RECORD DEER ARE INCREASING IN A REGION OF HIGH-QUALITY HABITAT

INTRODUCTION

Recent evidence suggests antlers of trophy white-tailed deer (*Odocoileus virginianus*) have been getting smaller across North America (Monteith et al. 2013). The hypothesized reason for this trend is that harvest by hunters is non-random, and hunters are increasingly interested in opportunities to harvest mature bucks (Connelly et al. 2012). Antler characteristics of white-tailed deer are heritable (Harmel 1983, Allendorf and Hard 2009, Webb et al. 2012), thus nonrandom harvest by hunters for these characteristics could have genetic implications via artificial selection. Examples of artificial selection have been reported in terrestrial and aquatic systems (Allendorf and Hard 2009). In bighorn sheep (*Ovis canadensis*) selection and harvest of trophy animals has led to smaller horn characteristics (Allendorf and Hard 2009, Monteith et al. 2013). Moreover, exploitation of fisheries tends to impose selection that alters fitness and population viability characteristics (e.g., smaller body sizes and lower reproductive productivity) by removing the older and larger fish (Allendorf and Hard 2009). Strickland et al. (2001) simulated the effects of selective harvest criteria based on antler characteristics on antler size. They found that antler characteristics can be used as selective harvest criteria, but widespread application of these criteria may have differing efficiencies across landscapes, due to changes in social and environmental conditions affecting antler growth and development (Strickland et al. 2001).

However, genetics is not the only factor affecting antler size. Antler growth in white-tailed deer depends primarily on the age, nutritional intake, and genetic potential of the individual deer (Demarais and Strickland 2011). Other factors such as condition of the mother, date of birth, health of the individual, and weather conditions may affect body condition and influence antler development (Garroway and Broders 2005, Monteith et al. 2009, Simard et al. 2014). These other factors may have a stronger influence at regional and local geographic scales. Deer are highly adaptable to a variety of landscapes and do well in fragmented habitats (Stewart et al. 2011). Previous studies have shown differences in conditions and characteristics of deer populations from diverse habitats (Hewitt 2011, Demarais and Strickland 2011 and references therein). In Mississippi, antler development was greatest in regions of greater soil fertility (Strickland and Demarais 2000). Areas of greater nutrition allowed deer to grow larger antlers at younger ages relative to other soil regions (Strickland and Demarais 2000). Variation in antler size has also been attributed to differences in composition of land cover types (Strickland and Demarais 2008).

Patterns of variation in antler size and conformation of deer are noticeable when considering geographic regions (Demarais and Strickland 2011), suggesting that processes influential to antler formation vary spatially. However, regional analyses of antler sizes in white-tailed deer with antlers that qualify for entry in the Boone and Crockett records (hereafter referred to as record deer) are lacking. Moreover, it is unclear whether the declining trend in antler size of all North American records of white-tailed deer reflects trends at smaller geographic scales. Therefore, the goal of this chapter was to understand regional trends and influences on antler sizes of record deer in the Midwest United States. The objectives were to 1) identify geographical areas where antler sizes of record deer were similar, 2) assess how antler sizes of record deer have changed through time in the Midwest United States, and 3) evaluate ecological influences on antler sizes of record deer.

STUDY AREA

This research included 9 Midwestern states (857 counties): Illinois, Indiana, Iowa, Kentucky, Michigan, Minnesota, Missouri, Ohio, and Wisconsin (Figure 2.1). The region covered 4 ecosystem provinces (Bailey 1983, Bailey 1995). Much of the Midwest consists of mixed agriculture and forested lands, which is high-quality habitat for an edge species such as white-tailed deer (Alverson et al. 1988). The topography across most of the study area is rolling, but there are some areas with irregular, more rugged terrain (Bailey 1995). The ecoregions with rugged terrain within study area include Central Appalachians, Driftless Area, Interior Plateau, Ozark Highlands, and Western Allegheny Plateau (Omernik 1987, Wiken et al. 2011). The Laurentian mixed forest province characterized the north, the east was characterized by the eastern broadleaf forest (oceanic) province, the south-central region was portrayed by the eastern broadleaf forest (continental) province, and the west-central region was characteristic of the prairie parkland (temperate) province. Furthermore, vegetation of the north, east, and south central were characterized by forests, while the west-central vegetation was described as forest-steppe. A variety of forest species are found throughout the study area including maples (*Acer* spp.), oaks (*Quercus* spp.), hickories (*Carya* spp.), and spruce (*Picea* spp.) trees (Omernik 1987, Bailey 1995, Pierce et al. 2011, Wiken et al. 2011).

The climate of counties within the study area is a product of latitude and position relative to the Great Lakes. In general, as locations move farther away from the equator and closer to the poles winters become more severe. Average temperatures in the Northern Lakes and Forests ecoregion range from 2°C to 6°C, with an average of –10°C in the winter (Wiken et al. 2011). Annual temperatures are warmer in the Ozark Highlands where the average ranges from 12°C to 15°C (Wiken et al. 2011). The time available for crop production is known as the frost-free period. The northern extent of my study area has the fewest number of days available for crop production, with as few as 95–100 days available in the Lake Manitoba and Lake Agassiz Plain and Northern Lake and Forests ecoregions (Wiken et al. 2011). The Central Irregular Plains and Ozark Highlands ecoregions have some of the longest frost-free periods at 165–235 days and 140–230 days, respectively (Wiken et al. 2011). Nearly all the natural vegetation in the Eastern Corn Belt Plains, Central Corn Belt Plains, and Western Corn Belt Plains has been converted into cropland that mainly produces corn and soybeans. The Western Corn Belt Plains ecoregion is one of the most productive areas in the world for corn and soybeans (Wiken et al. 2011). Additional descriptions of the study area can be found in VerCauteren and Hygnstrom (2011).

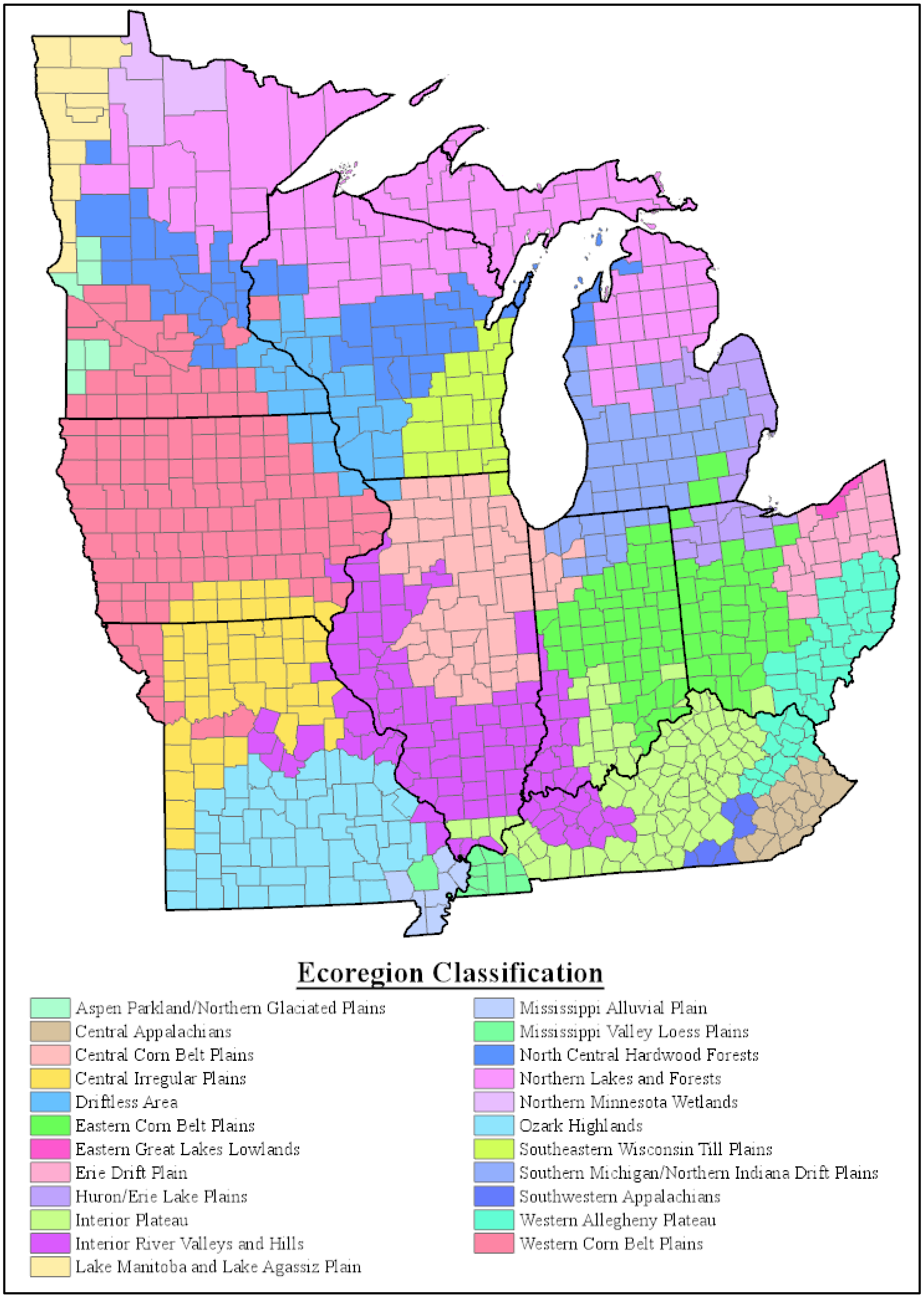

Figure 2.1 Map of ecoregion classification for each county in study area (Omernik 1987, Bailey 1995). I assigned an ecoregion to each county by determining which ecoregion covered the majority area within the county. These data are from 9 Midwestern states in the United States (Illinois, Indiana, Iowa, Kentucky, Michigan, Minnesota, Missouri, Ohio, and Wisconsin).

METHODS

Data on record deer were obtained from the Boone and Crockett Records of North American Big Game. The Boone and Crockett Club established a standardized system for measuring and scoring big game in North America and maintained the data to serve as a baseline for future studies that investigate trends in record animals (Nesbit and Wright 2016). The system was designed to emphasize bilateral symmetry by penalizing the net score based on the amount of asymmetry; the non-typical category was developed to recognize deer with unusually large amounts of abnormal growth. Detailed measurements of antler characteristics and specific calculations produce a numerical net score that serves to rank the animals of a particular category (Reneau et al. 2011). I focused on records of white-tailed deer from 2 categories recognized by the Boone and Crockett Club, typical white-tailed deer and non-typical white-tailed deer that were harvested in the Midwestern United States from 1973–2014. In general, typical record deer have very few or no abnormal points, whereas the antlers of nontypical deer are characterized by numerous abnormal points (Nesbit and Wright 2016). I limited my assessment to records from this time frame because 1973 was the first year that the Boone and Crockett Club began quality control measures for the records (personal communication, Jack Reneau, Director of Records for the Boone and Crockett Club, 30 June 2015). Thus, any records submitted after 1972 were verified for accuracy before being accepted into the record book.

Measurements of typical deer and nontypical deer are the same; however, the 2 categories differ in how they incorporate abnormal points into the final score (Nesbit and Wright 2016). Unlike the final score, the calculations for gross score are indistinguishable between the categories of record deer. The gross score is the sum of the antler measurements and does not include penalties (i.e., score deductions) for non-symmetry (Nesbit and Wright 2016). Therefore, I used gross score as my response variable because it is more representative of the total amount of antler grown. The Institutional Animal Care and Use Committee at Michigan State University determined that the acquisition of harvest data from the Boone and Crockett Club was exempt from protocols by the Animal Care and Use Committee. I followed guidelines outlined by the Boone and Crockett Club for securely processing and storing the data supplied for this research.

Climate data from weather stations were obtained from the National Oceanic and Atmospheric Administration's (NOAA) National Centers for Environmental Information (NCEI). I used monthly summaries datasets to portray total precipitation (mm) during the spring and summer months (PRECIP) and number of days with 2.54 cm or more snow on the ground (SNOW). These data were provided as points for each weather station. However, I do not know the exact point location where each record deer was harvested, so I used block kriging to interpolate the climate data for each county. I fit a variogram model to the climate data and predicted climate values from a kriged model (for prediction results see Figure 2.2 and Figure 2.3). This process was repeated for each year and both climate variables (package *gstat* v1.1-0, Program R v3.2.2, R Development Core Team.)

I used ArcGIS to reclassify the 2001, 2006, and 2011 National Land Cover Database (Fry et al. 2011) from 16 to 7 classes (i.e., agriculture, forest, rangeland, developed, wetlands, water, and other). Using the reclassified raster, I calculated landscape metrics in program FRAGSTATS (v4.1, University of Massachusetts, Amherst). The percent cover of the 7 land cover classes for each county was used to characterize the composition of the landscape, and the percent of forest cover (FOR) and percent of agriculture cover (AG) were used in analyses. The interspersion-juxtaposition index (IJI) and contagion value (CONTAG) for each county characterized the configuration of the 7 land cover classes.

I used the Soil Survey Geographic Database (SSURGO) to quantify the National Commodity Crop Productivity Index (CPI) model for each county. Crop productivity is an interpretation of the capacity for soils, landscapes, and climates to produce non-irrigated commodity crops such as corn, soybeans, grains, and cotton (Dobos et al. 2008). I used the coefficient of variation (CV) for the crop productivity value within each county to represent variation in the productivity index. I assumed that variation in crop productivity was important at the county-level because suitable habitat for deer includes mixing of agricultural and non-agricultural (i.e., forested) land (Cain et al. 2019). Moreover, previous research has shown that differences in soil attributes can lead to variation in antler characteristics (Strickland and Demarais 2000).

I calculated the variance inflation factor (VIF) for the full set of potential variables to assess which variables were highly related (Zuur et al. 2007) and used the backward selection process to remove variables until VIF values of all remaining variables were low ($VIF < 3$, Zuur et al. 2009). I also used correlation matrices to determine the degree of collinearity in explanatory variables. I considered 2 explanatory variables to be collinear when the correlation coefficient was high ($r \geq |0.5|$, Program R v3.1.3, R Development Core Team).

The first step I took toward understanding how sizes of antlers change through time and vary across the Midwest was to determine if there were areas with similar antler sizes. To assess trends in identifying the appropriate grouping method for record deer in the Midwest, I categorized counties using three *a priori* variables: County (no grouping), State (IA, IL, IN, KY, MI, MN, MO, OH, or WI), and Level 3 Ecoregion (Bailey 1995). For counties crossing ecoregion boundaries, I used the majority ecoregion type within the county (Figure 2.1). For each category, I evaluated 2 random effects structures for variable groupings, the random intercept model and the random intercept and slope model (Zuur et al. 2009, Table 2.2). Models were fit using the *lme4* package in R (version 3.6.1). The random intercept model assumes that the groups follow the same trend in antler size over time but there is variation in antler size among the groups. The random intercept and slope model assumes that groups vary in antler size and follow different trends in antler size over time. If the random intercept and slope structure fits best, it would provide evidence of variation in the magnitude or direction of trends in antler size across space. I used Akaike's Information Criterion with correction (AIC_c) for small sample size to evaluate the set of model structures for each grouping method (Gelman and Rubin 1992). Models with ΔAIC_c values between 0–2 were competing models for explaining the underlying structure of the data (*AICcmodavg* package, R version 3.2.2).

To test hypothesized relationships between antler sizes and environmental characteristics, I developed 9 linear mixed-effects models using the random effects structure with the most support. The hypotheses I tested were different combinations of year, soil, climate (snow days and precipitation), and landscape (percent forest, interspersion-juxtaposition index) covariates (see Table 2.2). I fit the 9 models using the *lme4* package in R (version 3.2.2). I considered any model with ΔAICc values between 0–2 to be competing models for explaining the data (*AICcmodavg* package, R version 3.2.2). I created a line graphs to display changes in antler size through time, and to visualize the spatial relationships with results from the top-ranking model. Additionally, a map was produced to demonstrate group-level differences in mean antler sizes of record deer.

RESULTS

I analyzed records for 2,900 nontypical deer and 2,846 typical deer from the Boone and Crockett Records of North American Big Game from 1973–2014. Gross scores of all record deer included in this analysis ranged from 434.0–863.6 cm, with an average antler size of 505.7 cm (*SD* = 46.6). The percent of agriculture cover (AG) was omitted from further analysis due to VIF value above the cutoff. The 2 landscape configuration variables were collinear, thus the contagion value (CONTAG) was also omitted from further analysis. The following 6 variables were included in subsequent analyses: year of harvest (YEAR), percent of forest cover (FOR), interspersion-juxtaposition index (IJI), number of days where snow depth was 2.54 cm or more (SNOW), total precipitation during the spring and summer months (PRECIP), and variation in the crop productivity index (CPI_CV).

I found that the intercept-only random effect structure for the ecoregion model was the best supported (ΔAIC_c = 0.00, weight = 0.87), and the state and county models received minimal support (Table 2.1). Among the 6 candidate models used to evaluate an appropriate random effects structure, I found consistent support for models using the Intercept-only temporal random effects structure regardless of grouping method (Table 2.1). Therefore, I used the intercept-only structure with a random effect with grouping by ecoregion to evaluate environmental factors influencing gross scores of record deer through time. Records were not evenly distributed among ecoregions (Figure 2.4).

For the environmental analysis, I found 4 competing models, indicating some support for 4 of the hypotheses that I tested (Table 2.2). Competing models included the Habitat (ΔAIC_c = 0.00, weight = 0.26), Landscape (ΔAIC_c = 0.05, weight = 0.26), Recent model (ΔAIC_c = 0.15, weight = 0.24), and Full models (ΔAIC_c = 0.29, weight = 0.23, Table 2.3). Variables included in all competing models (i.e., YEAR [$\beta = 0.16$, 0.16, 0.15, and 0.17], FOR [$\beta = -3.08$, -3.02, -3.05, and -3.05], and IJI [$\beta = -1.03$, -0.94, -0.90, and -1.03]) had consistent effects on the response variable (Table 2.3, Table 2.4, Table 2.5, Table 2.6). I found a positive relationship between gross scores and YEAR ($\beta = 0.16$, SE $= \pm\, 0.06$, Figure 2.5), but the proportion of forest ($\beta = -3.08$, SE $= \pm\, 0.90$) and degree of agriculture-forest interspersion ($\beta = -1.03$, SE $= \pm\, 0.8$) were negatively associated with antler sizes for ecoregions (Table 2.3). Moreover, the best-supported models included the FOR and IJI covariates, whereas these covariates are not part of the remaining models. Mean antler sizes differed among ecoregions in the Midwest United States (range $= -9.27 - 10.61$ cm, Figure 2.6). The Driftless ecoregion had the smallest mean antler sizes (-9.27 cm) and the Erie Drift Plain ecoregion had the largest mean antler sizes ($+10.61$ cm).

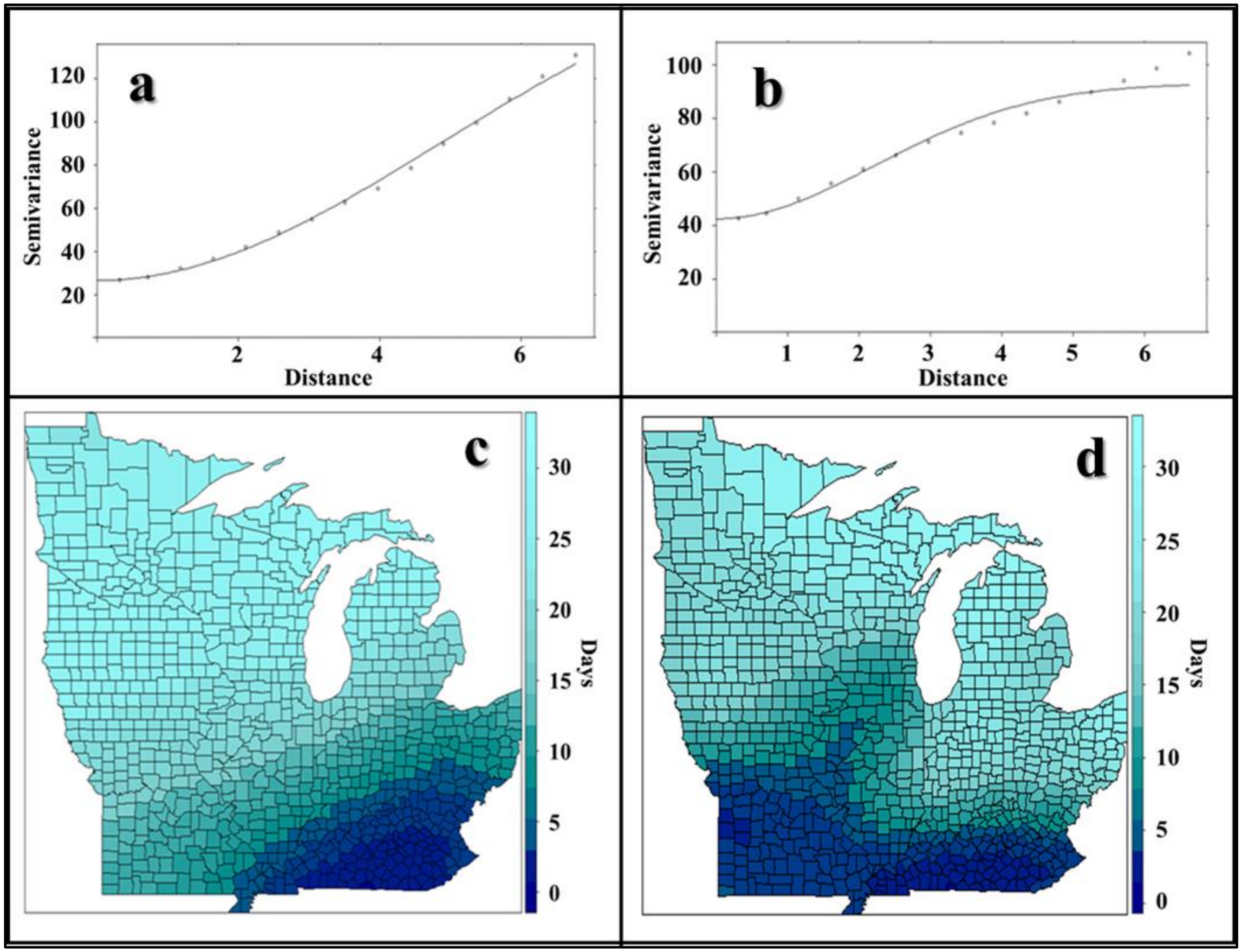

Figure 2.2 Variograms and county-specific prediction maps for years 1984 and 2004 for the number of days where snow depth was 2.54 cm or more (SNOW). The darker shade indicates fewer days where snow depth was one or more inches. These data are from 9 Midwestern states in the United States (Illinois, Indiana, Iowa, Kentucky, Michigan, Minnesota, Missouri, Ohio, and Wisconsin). (a) 1984 variogram is a Gaussian model with nugget = 26.54, sill = 187.48, and range = 6.87. (b) 2004 variogram is a Gaussian model with nugget = 42.43, sill = 93.07, and range = 3.15. (c) Plot shows predicted number of days in 1984. (d) Plot shows predicted number of days in 2004.

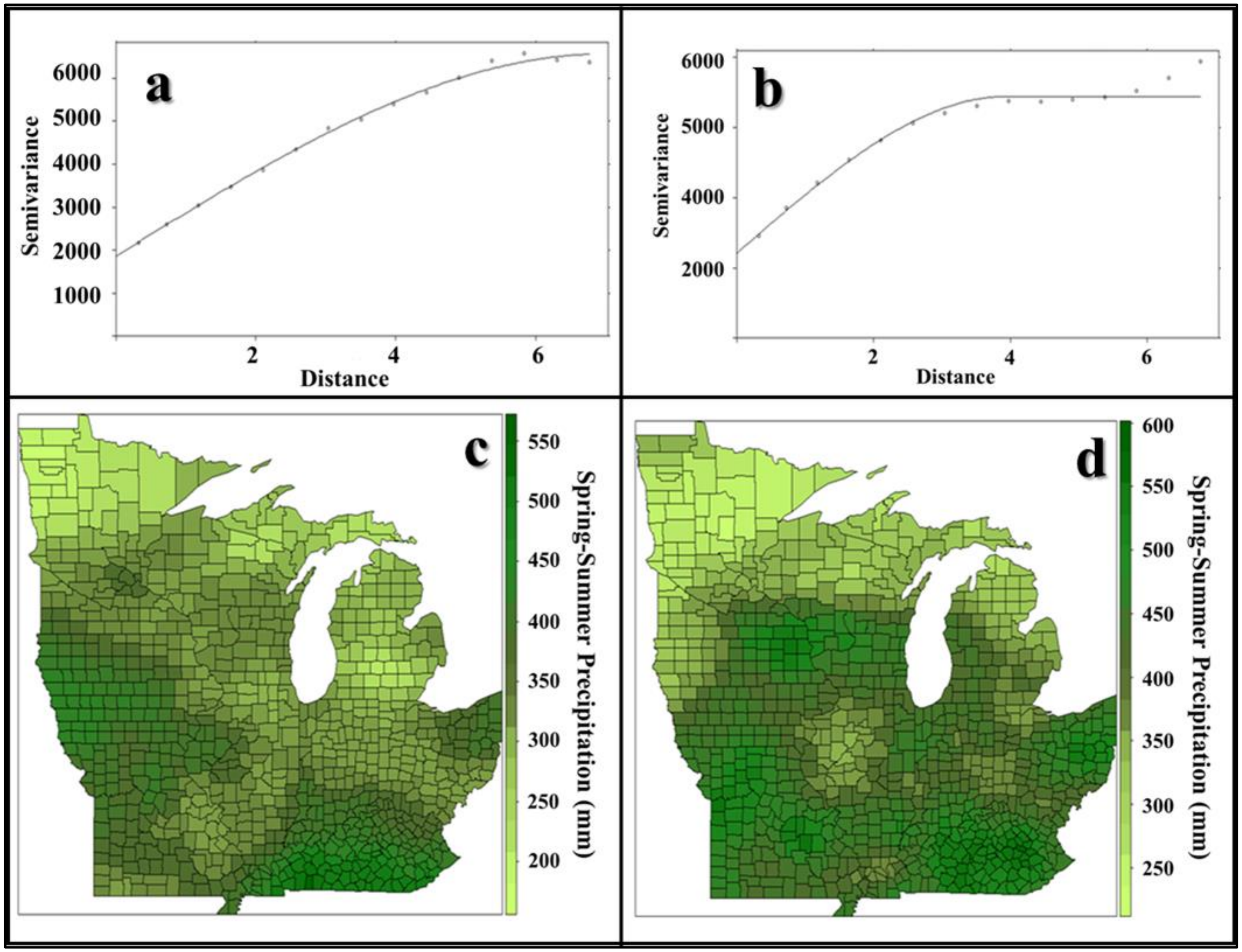

Figure 2.3 Variograms and county-specific prediction maps showing total precipitation for years 1984 and 2004 during the spring and summer months (PRECIP). The darker shades indicate greater precipitation during the spring and summer months. These data are from 9 Midwestern states in the United States (Illinois, Indiana, Iowa, Kentucky, Michigan, Minnesota, Missouri, Ohio, and Wisconsin). (a) 1984 variogram is a Spherical model with nugget = 2,678.59, sill = 8,876.58, and range = 6.53. (b) 2004 variogram is a Spherical model with nugget = 3,618.99, sill = 8,035.93, and range = 4.97. (c) Plot shows predicted amount of precipitation in 1984. (d) Plot shows predicted amount of precipitation in 2004.

Table 2.1 Model comparisons evaluating random effects structure for identifying geographical areas where antler sizes of record deer have been similar in the Midwest United States from 1973–2014. Boone and Crockett records of white-tailed deer from Illinois, Indiana, Iowa, Kentucky, Michigan, Minnesota, Missouri, Ohio, and Wisconsin were included in the analysis.

Grouping Method	**Year Effect**	**ΔAIC_c**	**w_i**
Ecoregion	Random Intercept	0.00	0.87
Ecoregion	Random Slope + Intercept	3.91	0.12
State	Random Intercept	9.86	6.28E-03
State	Random Slope + Intercept	13.79	8.80E-04
County	Random Intercept	19.44	5.21E-05
County	Random Slope + Intercept	23.46	7.00E-06

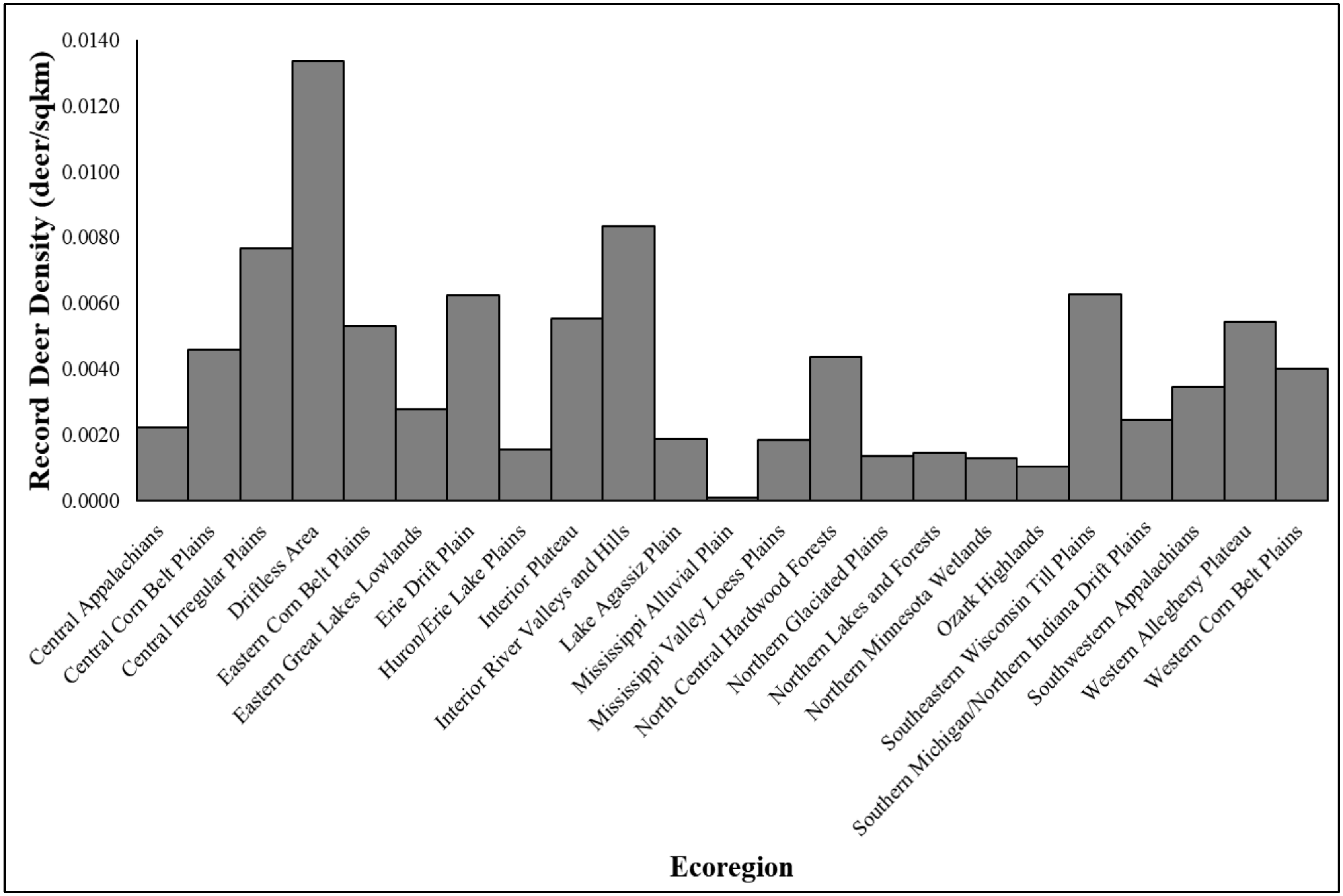

Figure 2.4 Distribution of density (deer/km^2) in record deer among ecoregions in the Midwest United States from 1973–2014. These data are from 9 Midwestern states in the United States (Illinois, Indiana, Iowa, Kentucky, Michigan, Minnesota, Missouri, Ohio, and Wisconsin).

Table 2.2 Model comparisons relating climate/weather, landscape composition, landscape configuration, and soil characteristics to the gross score (cm) of record white-tailed deer. Boone and Crockett records of white-tailed deer harvested in Illinois, Indiana, Iowa, Kentucky, Michigan, Minnesota, Missouri, Ohio, and Wisconsin during years of study (1973–2014) were included in the analysis.

Name	**Model****	**ΔAIC_c**	**w_i**
Habitat	GS ~ YEAR + FOR + IJI + CPI_CV	0.00	0.26
Landscape	GS ~ YEAR + FOR + IJI	0.05	0.26
Recent	GS ~ YEAR + FOR + IJI + PRECIP	0.15	0.24
Full	GS ~ YEAR + SNOW + PRECIP + CPI_CV + FOR + IJI	0.29	0.23
Seasonality	GS ~ YEAR + SNOW + PRECIP	11.10	0.001
Year	GS ~ YEAR	11.13	0.001
Historical	GS ~ YEAR + SNOW + CPI_CV	11.25	0.001
Soil	GS ~ YEAR + CPI_CV	11.60	0.001
Vegetation	GS ~ YEAR + PRECIP + CPI_CV	11.89	0.001

**Model Abbreviations: Gross score (GS), year of harvest (YEAR), percent of forest cover (FOR), interspersion-juxtaposition index (IJI), number of days where snow depth was 2.54 cm or more (SNOW), total precipitation during the spring and summer months (PRECIP), and variation in the crop productivity index (CPI_CV)

Table 2.3 Parameter estimates (β) ± Standard Error (SE) for the Habitat Model hypothesis, which states that the driving factors of antler size among record deer are habitat features and year. Boone and Crockett records of white-tailed deer harvested in Illinois, Indiana, Iowa, Kentucky, Michigan, Minnesota, Missouri, Ohio, and Wisconsin during years of study (1973–2014) were included in the analysis.

	β ± SE	**DF**	**t-value**	**p-value**
Intercept	191.01 ± 125.4	5719	1.52	0.13
YEAR	0.16 ± 0.06	5719	2.51	0.01
CPI_CV	0.66 ± 0.78	5719	0.86	0.39
FOR	–3.08 ± 0.90	5719	–3.41	0.001
IJI	–1.03 ± 0.80	5719	–1.35	0.18

Table 2.4 Parameter estimates (β) ± Standard Error (SE) for the Landscape Model hypothesis, which states that the driving factors of antler size among record deer are the configuration and composition of habitat and year, whereas the influences of climate and the longer-term impacts of nutrient cycling in the soil are negligible. Boone and Crockett records of white-tailed deer harvested in Illinois, Indiana, Iowa, Kentucky, Michigan, Minnesota, Missouri, Ohio, and Wisconsin during years of study (1973–2014) were included in the analysis.

	β ± SE	**DF**	**t-value**	**p-value**
Intercept	189.64 ± 125.3	5720	1.51	0.13
YEAR	0.16 ± 0.06	5720	2.52	0.01
FOR	–3.02 ± 0.90	5720	–3.37	0.001
IJI	–0.94 ± 0.80	5720	–1.25	0.21

Table 2.5 Parameter estimates (β) ± Standard Error (SE) for the Recent Model Hypothesis, which states that the driving factors of antler size among record deer are recent changes in habitat, weather, and year, whereas the longer-term impacts of nutrient cycling in the soil and climate are negligible. Boone and Crockett records of white-tailed deer harvested in Illinois, Indiana, Iowa, Kentucky, Michigan, Minnesota, Missouri, Ohio, and Wisconsin during years of study (1973–2014) were included in the analysis.

	β ± SE	**DF**	**t-value**	**p-value**
Intercept	207.15 ± 126.7	5719	1.64	0.10
YEAR	0.15 ± 0.06	5719	2.35	0.02
Precip	0.62 ± 0.65	5719	0.95	0.34
FOR	–3.05 ± 0.89	5719	-3.41	0.001
IJI	–0.90 ± 0.75	5719	-1.19	0.23

Table 2.6 Parameter estimates (β) ± Standard Error (SE) for the Full Model, which states that all covariates of interest, considered in this analysis, are driving antler size in the Midwest United States (i.e., Illinois, Indiana, Iowa, Kentucky, Michigan, Minnesota, Missouri, Ohio, and Wisconsin) during years of study (1973–2014).

	β ± SE	**DF**	**t-value**	**p-value**
Intercept	169.78 ± 142.7	5717	1.19	0.23
YEAR	0.17 ± 0.07	5717	2.35	0.02
SnowDays	0.50 ± 0.87	5717	0.58	0.56
Precip	0.59 ± 0.66	5717	0.90	0.37
CPI_CV	0.64 ± 0.78	5717	0.82	0.41
FOR	–3.05 ± 0.91	5717	-3.34	0.001
IJI	–1.03 ± 0.77	5717	-1.34	0.18

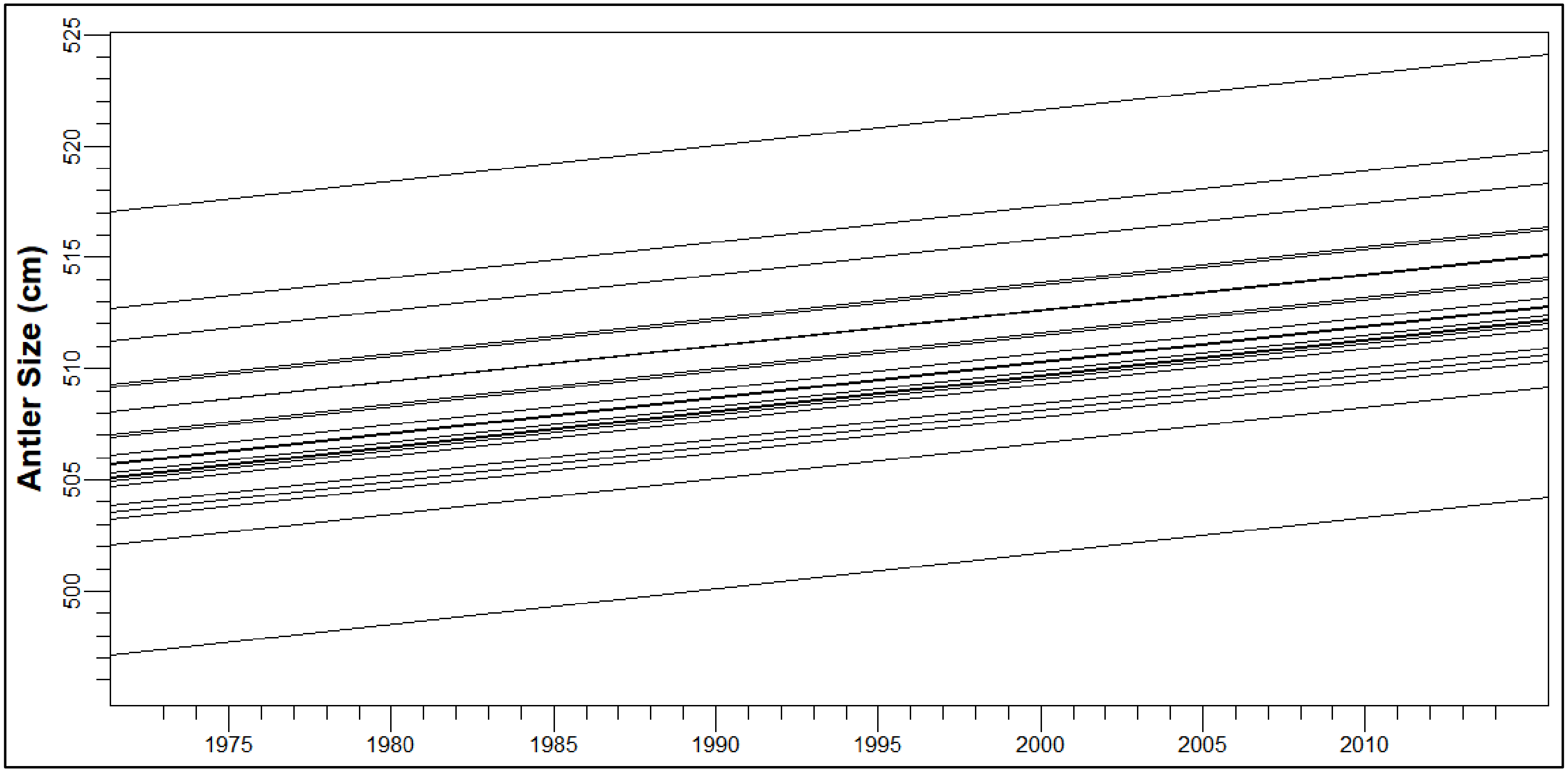

Figure 2.5 Trends in antler size of record deer for each ecoregion in across 9 Midwestern states in the United States (Illinois, Indiana, Iowa, Kentucky, Michigan, Minnesota, Missouri, Ohio, and Wisconsin). Each line has a positive slope (0.16 cm/year) with a unique intercept that represents the trend in the size of antlers for individual ecoregion from 1973–2014.

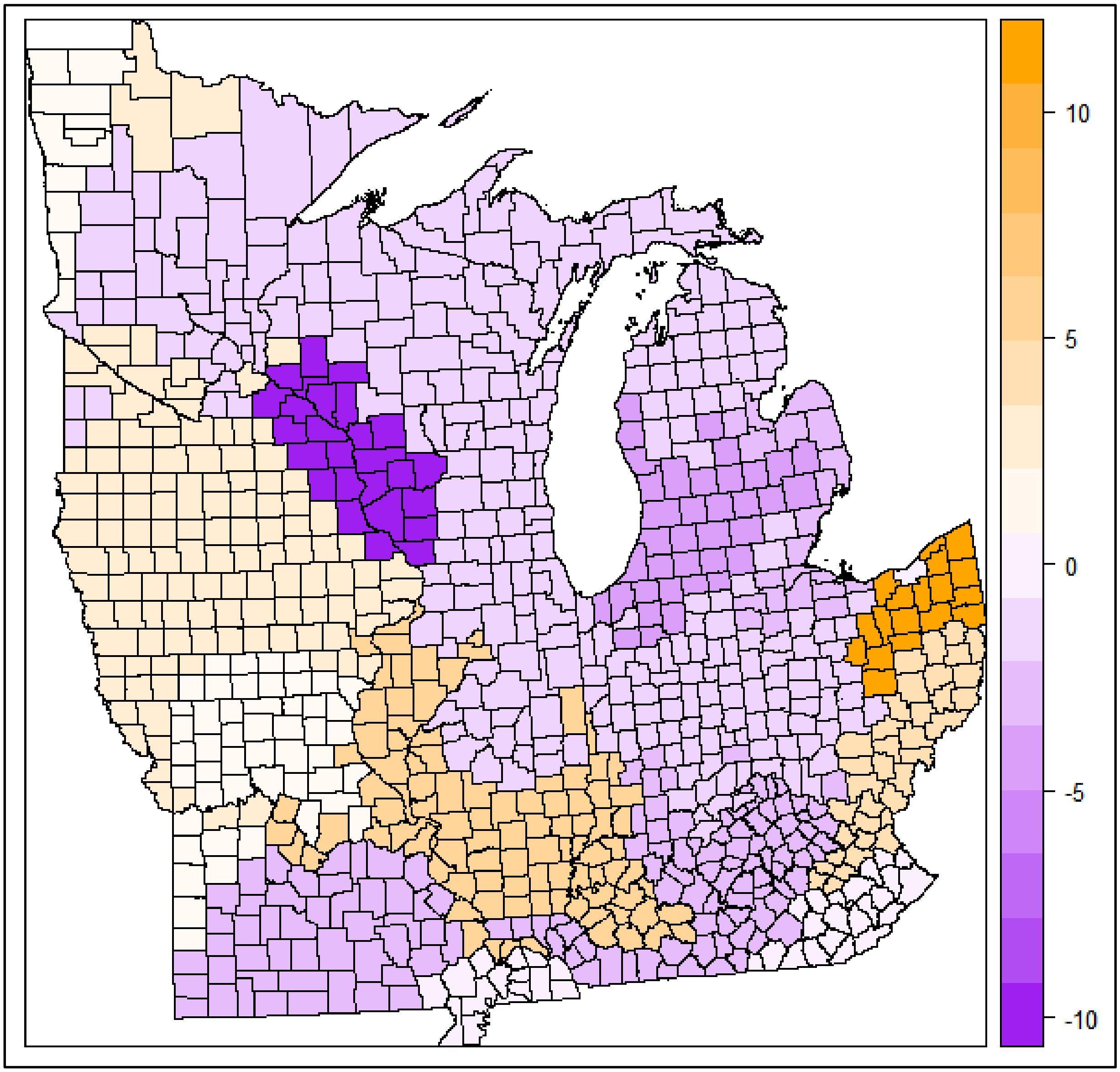

Figure 2.6 Magnitude and direction of change in mean antler sizes for each county relative to the average antler size of entire study area (1973–2014). Counties are grouped by which ecoregion covered the greatest amount of area within the county. This map shows that deer harvested in the western regions, southern Illinois, and eastern Ohio have larger antlers relative to other parts of the Midwest.

DISCUSSION

My findings underscored the importance of considering spatial and environmental context when investigating trends in wildlife populations. My results showed that antler sizes of record deer were most similar at scales relevant to ecoregions in the Midwestern United States. By grouping observations according to ecoregion and using the random intercept model, I was able to evaluate factors influencing trends in antler sizes of record deer and inherent differences in mean antler sizes among ecoregions. I found that antler sizes of record deer have been increasing in the Midwest since 1973. My findings also suggest that landscape factors were important for explaining antler size variability in record deer of the Midwestern United States.

The aggregation of antler sizes at the ecoregion-level suggests evidence of variation in antler sizes of record deer between different geographical contexts (Duncan et al. 1998). Ecoregions are characterized as areas with similar habitat and climate and can be useful toward addressing environmental issues and questions across large scales because they transcend political boundaries (Bailey 1995, Omernik 1995). I found no evidence that similarities in antler size of record deer in the Midwest were due to state- or county-level management strategies. My findings demonstrate that the spatial clustering of similar antler sizes through time is related to the ecoregion context rather than a management context. The resources available for antler growth influence the trends in antler size of record deer.

Record deer within the context of an ecoregion experience similar influences on antler size through time. Given the various patterns and processes that characterize the delineation of each ecoregion (Bailey 1995), I expected to find that antler sizes in some areas were increasing while antler sizes in other areas were decreasing. If trends in antler sizes were increasing in some areas of the Midwestern US while decreasing in others, I would have found greater support for the random slope and random intercept model. Instead, my results suggest that the random intercept model fit the data the best, indicating that trends in antler sizes among areas in the Midwestern US are trending at the same rate in the same direction (Figure 2.5). My finding that there is no evidence to support differing trends in antler size across the Midwest could be because (1) trends in antler size are not different or (2) sample sizes in individual ecoregions are small. The latter is an artifact of the modeling framework in which there is not enough data to detect varying trends among ecoregions. Therefore, the parallel trends across all ecoregions in the Midwest are a manifestation of the rigid structure imposed on the data under random intercept models (Duncan et al. 1998).

There is no single scale at which ecological phenomena should be studied (Levin 1992), and conclusions drawn from analyses of organisms at one scale may not be applicable at other scales (Wiens 1976, Turner 1989, Wiens 1989, Turner et al. 1995). At the continental scale, antlers of record deer appear to be getting smaller (Monteith et al. 2013), whereas my findings suggest that in the Midwest United States, antlers of record deer across all ecoregions are getting larger through time (Figure 2.5). Therefore, trends in antler sizes of record deer are not consistent across changing spatial scales. Similar conclusions were reported by Festa-Bianchet et al. (2015) that found the broad-scale conclusions in the Monteith et al. (2013) study did not reflect trends in horn sizes of a local population of big horn sheep (*Ovis canadensis*). If antler sizes are getting larger in the Midwest but declining overall, as suggested by Monteith et al. (2013), then antler sizes of record deer must be getting smaller elsewhere in North America. For a complete look at the trends across North America, spatially explicit analyses, like the one I present here, must be conducted for the remaining areas of the continent.

The increasing trend in antler size of record deer requires something to have been changing in the Midwest to cause antlers to get bigger. Antler growth in deer is driven by the genetic code, nutritional condition, and age of an individual (Monteith et al. 2009, Demarais and Strickland 2011). The harvesting of free-ranging white-tailed deer by hunters is a phenotypically nonrandom selection and previous studies disagree on how far the impacts reach. Some studies suggest selective harvesting of yearling males is not likely to influence the genetic potential of antler growth (low heritability, Lukefahr and Jacobson 1998, Webb et al. 2012, Hewitt et al. 2014, Webb et al. 2014), usually by citing the complex interactions of the environmental factors and the various injuries affecting antler development. Other studies suggest that selective harvest at young ages can impact the antler size of deer remaining in the cohort at later ages (Strickland et al. 2001, Lockwood et al. 2007, Hewitt et al. 2014, Ramanzin and Sturaro 2014), because of the relationship between yearling antler size and antler size at later ages. Given that record deer are harvested animals, I speculate that the increase in antler size is related to changes in cultural practice that interact with the high-quality habitat of the Midwest resulting in larger antlers. For example, there is a growing interest among hunters for regulations designed to produce more mature bucks (Ozoga et al. 1995, Cornicelli and Grund 2011, Connelly et al. 2012, Harper et al. 2012). Quality Deer Management (QDM) is a management paradigm focused on reducing yearling buck harvest and maintaining appropriate antlerless harvests to improve herd health and quality (Hamilton et al. 1995, Adams and Hamilton 2011). The decline of yearling males in the harvest is an indication of the spread of the management paradigm (Adams and Hamilton 2011). The percentage of yearlings in the male harvest is decreasing in the Midwest and other areas in the United States (Quality Deer Management Association [QDMA] Staff 2017). Moreover, forage quality for white-tailed deer is heterogeneous across space (Hewitt 2011), with a greater proportion of the Midwest providing high quality forage for white-tailed deer, relative to the proportion of suitable habitats across all of North America (VerCauteren and Hygnstrom 2011). Therefore, the interaction between practices and habitat (e.g., QDM practices in conjunction with good deer habitat) that leads to the increasing trend in antler sizes of record deer in the Midwest.

Record deer harvested in Iowa, southern Minnesota, southern Illinois, and eastern Ohio, have larger antlers relative to other parts of the Midwest (Figure 2.6). However, the greatest density of record deer was harvested from the Driftless ecoregion (Figure 2.4), which had the smallest antler sizes relative to other ecoregions. Therefore, areas where record deer were harvested regularly were not necessarily the areas producing deer with the largest antlers. Differences in average antler sizes could represent how energy demands of deer can vary among ecoregions, and what it means for offspring in area, as evidenced by the long-lasting consequences of deficient maternal investment. The environmental conditions experienced by male deer during gestation and early in life can have life-long influences on growth and development (Verme and Ullrey 1984, Monteith et al. 2009). Energy demands are greatest for female deer during pregnancy and lactation (Hewitt 2011). Deer are ruminants, and physical limitations of their digestive track impose limitations on forage intake (Ditchkoff 2011, Hewitt 2011). The daily energy requirements of lactation exceed the amount of food that females can ingest. To meet the energy costs for reproduction despite intake limitations, lactating females must sacrifice body condition and metabolize stored nutrients to provide offspring with resources for growth (Hewitt 2011). Although it is uncommon for females to produce antlers, there is evidence that the nutritional condition of females (i.e., maternal effects) in a population can be a driving factor in the body and antler sizes of males (Monteith et al. 2009). Monteith et al. (2009) showed that deer born to females in poorer condition showed reduced antler sizes. Deficient nutrition early in life can have lasting impacts on the growth and development of deer, even if those deer have access to high-quality forage. Therefore, the differences in antler sizes among ecoregions may represent disparities in the initial condition of male offspring.

Any model that included landscape configuration (IJI) and composition (FOR) covariates was competitive, which suggests that landscape factors were important for explaining antler size variability. In Mississippi, Strickland and Demarais (2008) reported that landscape composition explained variation in antler characteristics. My results support these findings, because IJI was not statistically significant. The negative relationship between proportion of forest and antler size suggests some interesting possibilities: (1) deer antlers are not able to grow as large on deer occupying densely forested areas or (2) deer with large antlers are less likely to be harvested in heavily forested areas. Forests provide woody vegetation that deer use for cover (Stewart et al. 2011), which protects deer from predators and hunters. Forest cover has been shown to decrease the amount of forage biomass available to deer (Stransky 1969, Conroy et al. 1982). In addition, my forest cover covariate shared an inverse relationship with percentage of agriculture in Midwest ($|r| > 0.90$). Therefore, the negative relationship between antler sizes and the amount of forest cover could represent that deer antlers grow larger when an area is dominated by agriculture. This interpretation would align with previous work showing that early successional forage improves phenotypic quality of deer (Strickland and Demarais 2008, Simard et al. 2014).

In this chapter, I sought to understand how antler sizes of record deer changed through time and across space. This spatial component produced findings potentially of interest to managers and ecologists. My analysis of record deer harvests in the Midwest United States showed that antler sizes have been increasing across this region of high-quality deer habitat since 1973. This result contrasts with findings of previous work that reported a decline in the antler sizes of record deer in North America over the last 100-years (Monteith et al. 2013). These conflicting results can be explained by differences related to scale and habitat between the studies. Managers may find the findings from this chapter useful when communicating with hunters or landowners about their expectations for the deer in the area. Moreover, because the differences in average antler sizes followed ecological delineated boundaries, rather than political boundaries, future studies using record deer might consider including these measures of ecological patterns and processes. The findings I report in this chapter are useful beyond the ecology and management of record deer, as support for the critical importance of scale considerations in ecological research.

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CHAPTER 3: MANAGEMENT INFLUENCES ON THE NUMBER OF WHITE-TAILED DEER IN THE BOONE AND CROCKETT RECORDS

INTRODUCTION

Harvest of deer by hunters is a non-random selection process and constrained by hunting regulations (Connelly et al. 2012). Variation in antlers can be observed throughout the distribution of white-tailed deer (*Odocoileus virginianus*), where differences in antler conformation and size are noticeable across landscapes (Demarais and Strickland 2011). White-tailed deer with antlers that qualify for entry in the Boone and Crockett records (hereafter referred to as record deer) are conceivably the fittest and highest quality mates that females seek (Verme and Ullrey 1984, Pierce et al. 2012, Morina et al. 2018). Antler growth is condition-dependent (Andersson 1986) and primarily influenced by age, nutrition, and genetics of the individual deer (Harmel 1982, Goss 1983, Scribner et al. 1989, Brown 1990, Demarais and Strickland 2011). Antlers are energetically expensive to produce (Brown 1990), so large antlers may serve as an honest indicator of male quality (Zahavi 1975). Moreover, findings from previous research provide evidence that antler characteristics are a visual representation of an individual deer's genetic quality and current physical condition (Ditchkoff et al. 2001*a*, Ditchkoff et al. 2001*b*, Demarais and Strickland 2011, Landete-Castillejos et al. 2012). Males that can afford the physiological cost to produce large antlers are selected by females over males with smaller antlers (Morina et al. 2018).

Hunter selectivity is affected by management regulations (Mysterud et al. 2006, Festa-Bianchet and Mysterud 2018), and hunting older male deer seems to be increasing in popularity (Adams et al. 2011, Heffelfinger 2013) as indicated by expanding interest in Quality Deer

Management (QDM) programs (Connelly et al. 2012, Harper et al. 2012). Hunters and other stakeholders have become more politically active in the decision-making process of setting hunting regulations (Nie 2004). Hunters can encourage managers to implement regulations perceived to have a positive effect on their opportunity to hunt mature deer with large antlers, such as antler restrictions that are often used to minimize harvest of young males and increase average age of male deer in a population (Miller and Marchinton 1995, Connelly et al. 2012). Habitat composition (Strickland and Demarais 2008), soil quality (Strickland and Demarais 2000), and land-use configuration (Cain et al. 2019, Cain 2020 – Chapter 2) also have effects on antler size, thus harvest criteria based on antler morphology must be specific to the area where implemented to be effective.

Hunters that want to harvest a record deer tend go where deer with large antlers are expected (Adams et al. 2009, Barrientos 2014, Hayworth 2014). The pursuit of deer with large antlers has a unique place in the hunting community (Messner 2011). Every year, numerous local, statewide, and national antler-size contests occur (Bauer 1993). Antlered specimens are measured, scores are calculated, animals are ranked by local and national organizations, and deer with large antlers (e.g., antler sizes that meet the minimum requirement for Boone and Crockett record deer) are prized in these contests. Although the Boone and Crockett records can be used to locate counties, states, and regions with frequent entries (Demarais and Strickland 2011, Barrientos 2014, Spring 2014), research to understand the spatial and temporal influences on the distribution of record deer is limited. Therefore, the question that remains is how management regulations have influenced the number of record deer. Moreover, it is unclear whether the occurrence and frequency of record deer reflects variation in site-specific conditions (e.g., soil fertility, composition of land-use types, winter severity), a temporal lag from the presence of a record deer in previous year, or both. Therefore, my goal for this chapter was to understand how geographic location, temporal autocorrelation, and management influence the number record deer in the Midwest United States. The objectives of my analysis were to 1) evaluate the relative change in harvests of record deer among ecologically relevant areas, 2) estimate the impact of having a record deer in the previous year, and 3) evaluate the relationship between management strategies and the number of record deer. The spatially comprehensive and long-term nature of the data collected and maintained by the Boone and Crockett Club provides an opportunity to quantify relationships between management and harvest of record deer.

STUDY AREA

My research included record deer that were harvested across a large spatial extent (129,087,856-ha region) of 856 counties from 9 Midwestern states: Illinois, Indiana, Iowa, Kentucky, Michigan, Minnesota, Missouri, Ohio, and Wisconsin (Fig. 3.1). Menominee County, Wisconsin (FIPS: 55078), and St Louis City, Missouri (FIPS: 29510) were not included in the analysis. Menominee County, Wisconsin was excluded because the Native American tribes have authority to manage the deer in this area and are not required to report harvest or hunter information to the state agency.

The study area extended over 23 ecoregions (Figure 3.1, Omernik 1987, Bailey 1995), with forest cover being dominant in the north and south, and agriculture dominating the central portion of my study area (Fry et al. 2011). Most agriculture practices focused on corn and soybean production. The topography across most of the study area is rolling, but there are areas with irregular, more rugged terrain (Bailey 1995). The ecoregions with rugged terrain within study area include Central Appalachians, Driftless Area, Interior Plateau, Ozark Highlands, and

Western Allegheny Plateau (Omernik 1987, Wiken et al. 2011). The climate of counties within the study area is a product of latitude and position relative to the Great Lakes. For additional information about climate and seasonality of my study area, see descriptions by Kunkel et al. (2013).

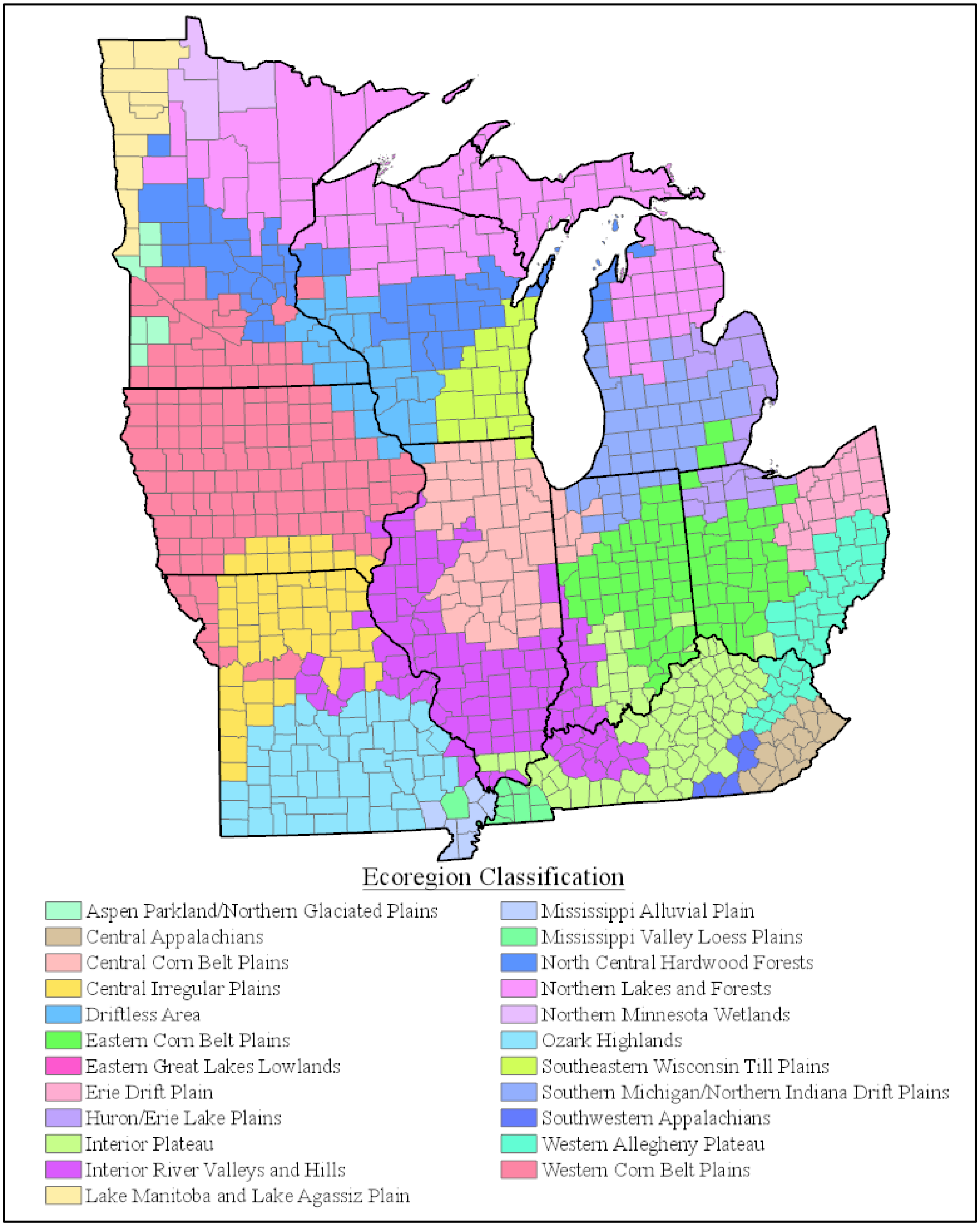

Figure 3.1 Ecoregion classification (Omernik 1987, Bailey 1995) for the counties of 9 states in the Midwestern United States included in my study area: Illinois, Indiana, Iowa, Kentucky, Michigan, Minnesota, Missouri, Ohio, and Wisconsin. I assigned an ecoregion to each county by determining which ecoregion covered the greatest amount of area within the county.

METHODS

Boone and Crockett Record Deer

The Boone and Crockett Club established a standardized system for measuring and scoring big game in North America and maintained the data to serve as a baseline for future studies to investigate trends in record animals (Nesbit and Wright 2016). The system was designed to emphasize bilateral symmetry by penalizing the final score based on the amount of asymmetry; detailed measurements of antler characteristics and specific calculations produce a numerical final score serves to rank the animals of a particular category (Nesbit and Wright 2016). For this analysis, I focused on records of white-tailed deer from 2 categories recognized by the Boone and Crockett Club, typical white-tailed deer and nontypical white-tailed deer, that were harvested in the Midwestern US from 1973–2014. In general, typical record deer have very few or no abnormal points, whereas the antlers of nontypical deer are characterized by numerous abnormal points (Nesbit and Wright 2016).

White-tailed deer recorded in the Boone and Crockett Club's Records of North American Big Game are examples of rare animals. The record deer that are reported represent a subset of all white-tailed deer with large antlers in the population. The Boone and Crockett Club relies on hunters to self-report and a network of trained volunteers (i.e., Official Measures) to generate biological data on harvested animals (Nesbitt and Wright 2016). Therefore, if social, economic, or other types of barriers impede hunters from registering a harvested deer, then that animal is less likely to be reported (see Appendix B). I obtained data for the record deer harvested during 1973–2014 from The Records of North American Big Game (Reneau et al. 2011). I limited my assessment to records from this time frame because 1973 was the first year that the Boone and

Crockett Club began quality control measures for the records (personal communications; Jack Reneau, Director of Records for the Boone and Crockett Club, 30 June 2015). Thus, any records submitted after 1972 underwent a more rigorous verification process to ensure the accuracy of biological data (e.g., measurements, calculations) before being accepted into the record book. I calculated the number of record deer reported annually in each county and used this information as my response variable in my spatially explicit models (Fig. 3.2).

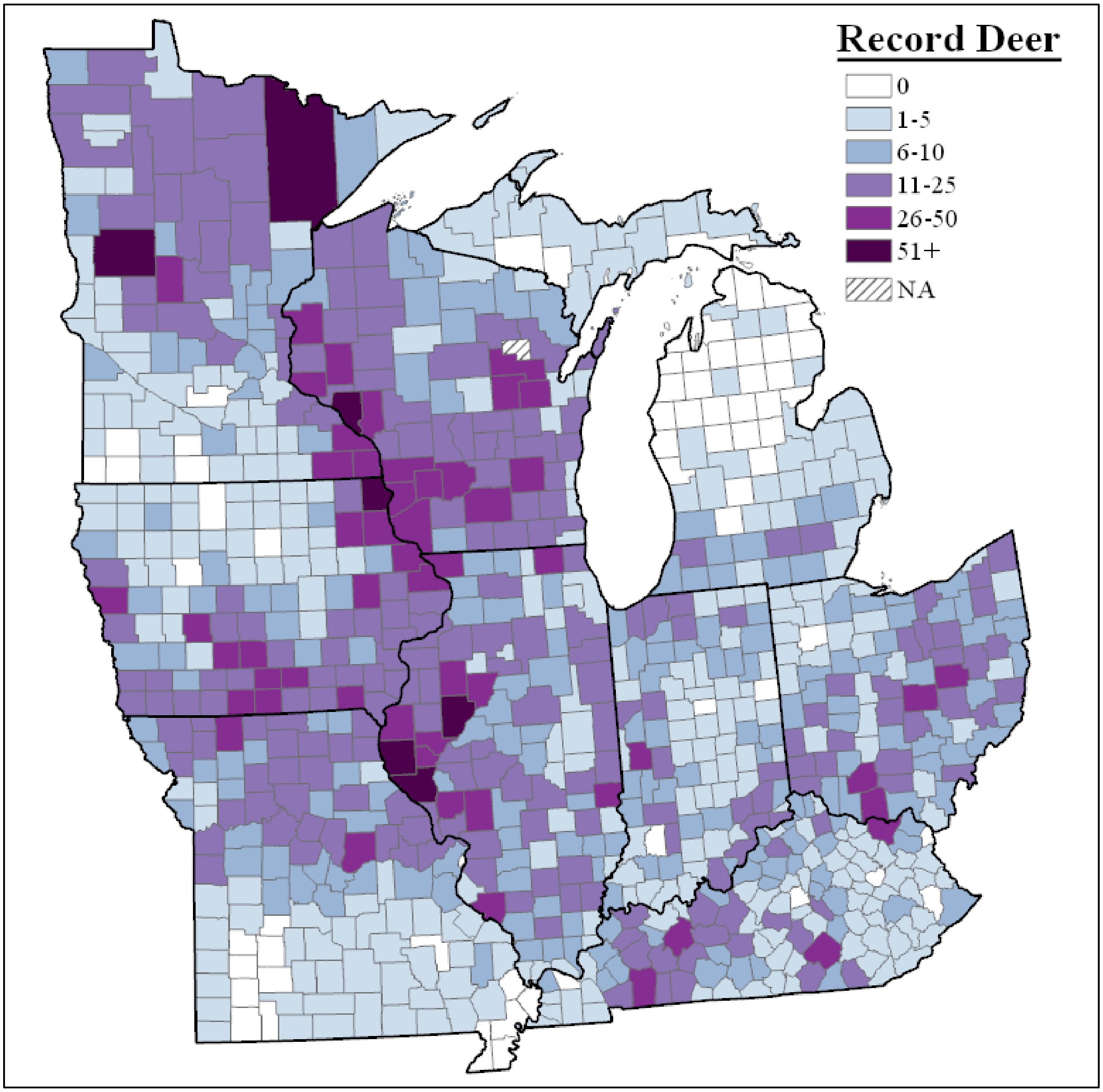

Figure 3.2 The number of Boone and Crockett record deer harvested in each county in the Midwestern United States from 1973–2014. My study area covered 9 states: Illinois, Indiana, Iowa, Kentucky, Michigan, Minnesota, Missouri, Ohio, and Wisconsin.

Zero-inflated Poisson Model

To evaluate the relationships between management actions and occurrence of record deer I used a zero-inflated Poisson (ZIP) model (Lambert 1992) via the *jagsUI* package (version 3.6.1, R Core Team 2019). Zero inflation is appropriate when data contain more counts of zero than would be expected for a Poisson distribution (Zuur et al. 2009). Given how rare the harvest and reporting of record deer to the Boone and Crockett Club can be, the observed number of record deer harvests for each county and year is more likely to be zero than any other number.

Under the ZIP model, counts of record deer were modelled as a mixture of a Bernoulli distribution and a Poisson distribution, and zeros were possible at both levels. I chose the ZIP model over the hurdle (i.e., zero-truncated) model, because I wanted to account for the issues surrounding imperfect detection of record deer by the Boone and Crockett records. I presumed that some of the zero-counts of record deer were due to characteristics of the county that made it unsuitable for producing record deer (i.e., true or structural zeros). However, I also recognized that some of the zeros could be due to imperfect detection (i.e., false zeros). The ZIP model helped account for unknown factors that led to a record deer going undetected by allowing zero-counts under the Poisson process (Kéry and Schaub 2012).

The general format of the ZIP model I used to relate the number of record deer (C_i) of county *i* to a linear predictor of covariates:

$$w_i \sim Bernoulli(\psi)$$

$$(C_i | w_i = 1) = w_i * \lambda_i$$

$$\log(\lambda_i) = \alpha + \beta_{TAuto} * TAuto_i + \beta_{Buck\_limit} * Buck\_limit_i + \beta_{APR} * APR_i + \beta_{Season\_length} * Season\_length_i + \gamma[Ecoregion_i],$$

where w_i is the outcome of a Bernoulli distribution that determines if the observation i (county during a particular year) is suitable for record deer with probability ψ. If the observation is suitable for record deer ($w_i = 1$), then the number of record deer harvested for a county during a particular year is determined by next level in the hierarchy. λ_i is the expected mean of suitable sites as a function of covariates on the link scale.

To assess the spatial distribution in the number of record deer harvested I included a random effect for ecoregion of the county ($\gamma[Ecoregion_i]$). To measure the temporal autocorrelation in the harvest of record deer, I used a covariate (*TAuto*) to represent the status of records in the previous year. *TAuto* was a binary variable, and a value of 1 was given if there was a record deer reported in the Boone and Crockett records the year before, otherwise a value of 0 was assigned for the county and year. The variable was included to account for possible sociological influences in reporting patterns through time. I predicted that a correlative temporal relationship existed in record deer by county, dependent on the presence of a record deer appearing in the previous year.

To evaluate the effects management regulations on the harvest of record deer in the Midwest United States I included three covariates representing various hunting regulations (*Buck_limit*, antler point restrictions [*APR*], and *Season_length*). The *Buck_limit* variable represents the maximum number of antlered males that a hunter may take annually. In some cases, the maximum number of antlered deer a hunter could harvest depended on the type of license they purchased. In such cases, the *Buck_limit* was always the greatest number of antlered deer that a hunter could harvest annually. Hunters were able to harvest 1 to 4 antlered deer annually depending on the county and year they hunted. *APR* was a binary variable. A value of 1 was given to counties during years that an antler point restriction was implemented, and a value of zero was given when antler point restrictions were not implemented in the county during the year. The *Season_length* was the length in days of the gun and muzzleloader seasons (*range* = 6–33 days). I included this variable, because the length of the season has a direct effect on total hunting opportunity. Shorter seasons do not provide as many opportunities (hunting days) as longer seasons. Moreover, the presence of hunters in the field influences deer movements (Little et al. 2014). To make model-fitting process more efficient, I standardized the values for Season Length and Buck Limit. Estimates from the model were based on 3 MCMC chains of 40,000 iterations. After a burn-in of 3,000 iterations with a thinning rate of 10 iterations yielded 11,100 total samples from the joint posterior.

The Institutional Animal Care and Use Committee at Michigan State University determined that the acquisition of harvest data from the Boone and Crockett Club and state agencies was exempt from protocols by the Animal Care and Use Committee. I followed guidelines outlined by the Boone and Crockett Club for securely processing and storing the data supplied for this research.

RESULTS

A total of 8,236 record deer were harvested and reported to the Boone and Crockett Club over the course of the study period (1973–2014). There were 29,949 (83.3%) county years with 0 counts. The other 6,013 (16.7%) county years had at least 1 record deer harvested and averaged 1.37 record deer (SD = 0.78). In 2010, Buffalo County, Wisconsin had 13 record deer, which is the largest count record for a single year. $\hat{R}$ values indicated that the model successfully converged (Table 3.1), because all the $\hat{R}$ values were < 1.1 (Kéry 2010, Gelman et al. 2013).

When I assessed the spatial distribution of record deer, I found that the number of record deer in a county year differed by ecoregion with 6 ecoregions above average (positive intercept) and 6 ecoregions below average (negative intercept) when the average number of record deer across the entire Midwest was set to zero (Fig. 3.3, Table 3.2). There were 8 ecoregions with numbers of record deer less than the Midwest average and 14 ecoregions with greater harvests of record deer than the Midwest average. Counties in the Central Appalachians ecoregion had the fewest record deer harvested (0.23 deer/year, credible interval [CI]: 0.10–0.45) relative to the Midwest average, whereas the average number of record deer was greatest in counties of the Driftless Area ecoregion (3.26 deer/year, CI: 2.49–4.29).

The status of records in the previous year proved to be a positive predictor of record deer in the Midwest United States. When I measured the temporal autocorrelation of record deer in the Midwest, I found a positive relationship between the number of record deer and the existence of an entry in the previous year (Table 3.1). The number of record deer was on average 2.76 more deer (CI: 2.62–2.90) when there was an entry the previous year.

When I evaluated the effects of management regulations on the harvest of record deer, I found evidence for a significant effect (Table 3.1). Negative predictors of record deer included the length of the hunting season (*Season_length*, mean change = 0.71 record deer, CI: 0.68–0.74) and the annual limit of antlered deer (*Buck_limit*, mean change = 0.82 record deer, CI: 0.79–0.85) for each county. For every 1-day increase in season length, the number of record deer decreased by 0.71 on average. For every 1-buck increase in the limit, the number of record deer decreased by 0.82 on average. The magnitude of predictive strength for *Season_length* was greater than the strength of the relationship between *Buck_limit* and record deer. The results from my model suggested that fewer record deer would be harvested from areas with longer seasons or more liberal bag limits for antlered deer. The presence of antler point restrictions in an area proved to be a positive predictor of record deer (Table 3.1). The number of record deer harvested from areas with antler point restrictions averaged 1.60 more record deer (CI: 1.40–1.81 deer) than areas that did not have antler point restrictions.

Table 3.1 Parameter estimates and associated 95% credible intervals (LCI: Lower Credible Interval, UCI: Upper Credible Interval) from zero-inflated Poisson model for the number of record deer harvested in the Midwest United States (1973–2014). $\hat{R}$-values indicated that the model successfully converged. Data for analysis included record deer harvested in Illinois, Indiana, Iowa, Kentucky, Michigan, Minnesota, Missouri, Ohio, and Wisconsin.

Parameters[*]	$\boldsymbol{\beta}$	**LCI**	**UCI**	$\boldsymbol{\hat{R}}$	**n.eff**
Intercept (α)	-1.63	-1.89	-1.40	1.02	270
ψ	0.62	0.59	0.64	1.00	4,994
TAuto[**]	1.014	0.96	1.06	1.00	11,100
APR[***]	0.468	0.34	0.60	1.00	11,100
Buck_limit	-0.197	-0.24	-0.16	1.00	4,932
Season_length	-0.341	-0.38	-0.30	1.00	3,389

[*] Parameter Abbreviations: Model Intercept (α), psi (ψ) is the probability that a county year was suitable, *TAuto* represents the status of records in the previous year, Antler Point Restrictions (APR), *Buck_limit* represents the maximum number of antlered males that a hunter may take annually, *Season_length* was the length in days of the gun and muzzleloader seasons

[**] *TAuto* was a binary variable, and a value of 1 was given if there was a record deer reported in the Boone and Crockett records the year before, otherwise a value of 0 was assigned for the county and year

[***] *APR* was a binary variable, and a value of 1 was given to counties during years that an antler point restriction was implemented, and a value of zero was given when antler point restrictions were not implemented in the county during the year

Table 3.2 The number of counties included and estimated intercepts for each ecoregion based on a random effect for ecoregion with a mean of zero. I assigned an ecoregion to each county by determining which ecoregion covered the greatest amount of area within the county. Boone and Crockett records of white-tailed deer harvested in Illinois, Indiana, Iowa, Kentucky, Michigan, Minnesota, Missouri, Ohio, and Wisconsin during years of study (1973–2014) were included in the analysis.

Ecoregion Classification[a]	**No. Counties**	**Intercept (γ)**
Central Appalachians*	16	-1.472
Northern Lakes and Forests*	71	-0.807
Southern Michigan/Northern Indiana Drift Plains*	37	-0.760
Western Allegheny Plateau*	36	-0.676
Interior River Valleys and Hills*	96	-0.507
Northern Minnesota Wetlands*	3	-0.473
Ozark Highlands	47	-0.135
Mississippi Alluvial Plain	6	-0.025
Huron/Erie Lake Plains	21	0.038
Eastern Corn Belt Plains	84	0.046
Western Corn Belt Plains	119	0.057
Southeastern Wisconsin Till Plains	22	0.065
Mississippi Valley Loess Plains	9	0.066
Central Corn Belt Plains	46	0.095
Lake Agassiz Plain	10	0.137
Erie Drift Plain	19	0.262
Central Irregular Plains*	49	0.451
Northern Glaciated Plains*	6	0.515
North Central Hardwood Forests*	44	0.623
Southwestern Appalachians*	6	0.694
Interior Plateau*	85	0.805
Driftless Area*	26	1.191

[a] Ecoregions with an asterisk (*****) are significant. Significance was determined by a credible interval (CI) that did not include 0.

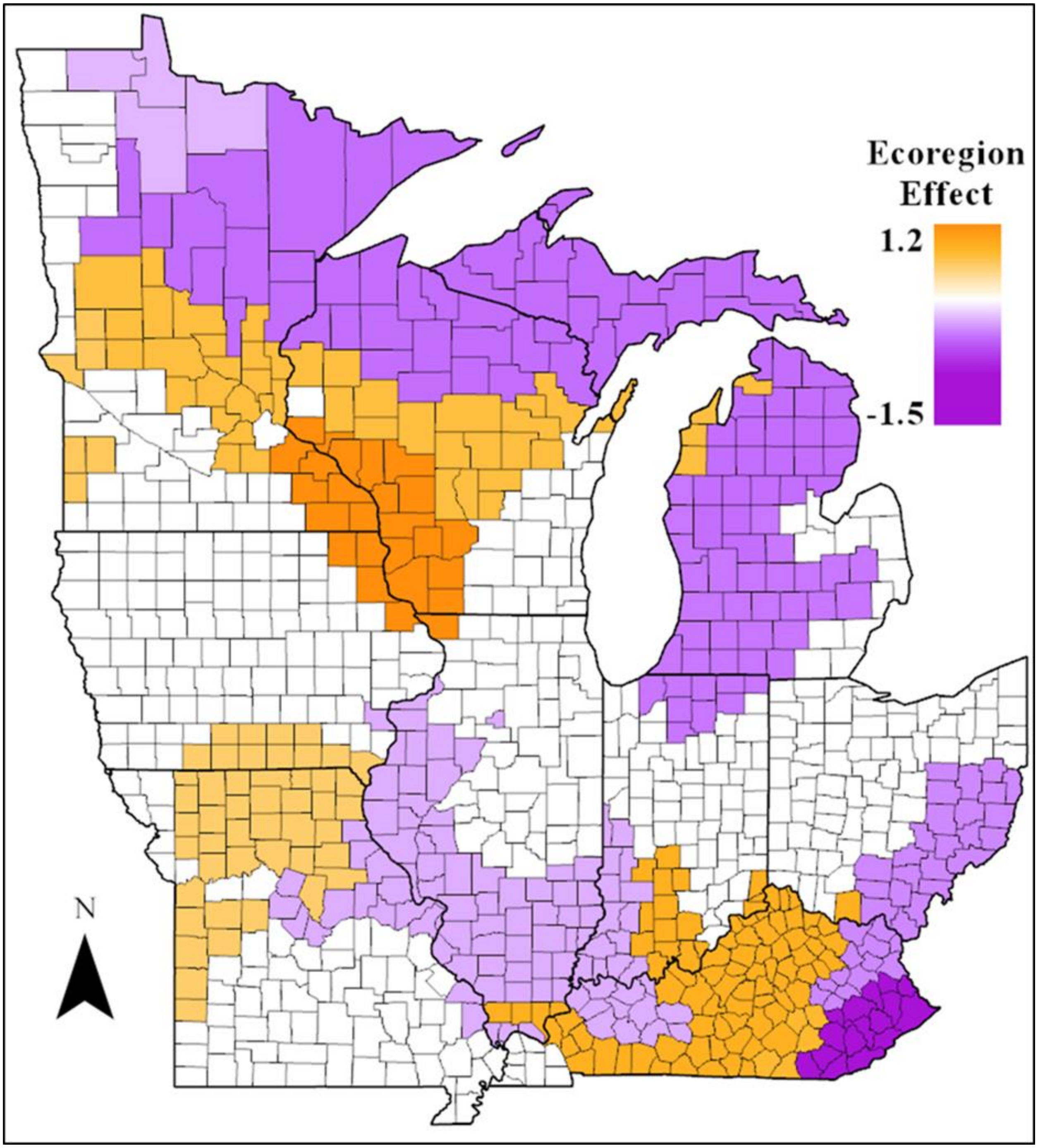

Figure 3.3 Map showing differences in the number of record deer among the ecoregions across the Midwest United States (i.e., Illinois, Indiana, Iowa, Kentucky, Michigan, Minnesota, Missouri, Ohio, and Wisconsin) during study (1973–2014). I assigned an ecoregion to each county by determining which ecoregion covered the greatest amount of area within the county. Purple areas are ecoregions with fewer record deer than expected from the zero-inflated Poisson model, whereas the orange areas correspond to ecoregions with more record deer than predicted given the model. Ecoregions that did not have a significant influence (i.e., credible interval included zero) on the number of record deer are white.

DISCUSSION

My findings provide information about the regional trends and influences on the number of record deer in the Midwestern United States. By grouping observations according to ecoregion, I found that characteristics within ecoregions influenced the number of record deer harvested and reported. My results showed that the average number record deer was greatest in the Driftless ecoregion and smallest in the Central Appalachians ecoregion. I found evidence for temporal autocorrelation in the records, with reporting the previous year having a positive influence on the number of record deer in the following year. My findings also suggest that management regulations were important for explaining variation in the number of record deer harvested and reported.

I focused on management variables in the model for this chapter but included a random effect for each ecoregion to account for the ecological and environmental differences among these areas. My results demonstrate that when the management covariates (i.e., *Buck_limit*, *Season_length*, and *APR*) are held constant, there is an ecoregion-level effect. This ecoregion effect could be related to the relationship between habitat quality and antler size demonstrated in previous studies. Antler growth and size are influenced by soil fertility (Strickland and Demarais 2000, Jones et al. 2010) and land-use types that promote or suppress early successional plants (Strickland and Demarais 2008, Cain 2020 – Chapter 2). Much of the Midwest consists of mixed agriculture and forested lands, which is high-quality habitat for an edge species such as white-tailed deer (Alverson et al. 1988). Ecoregions with positive influences on the number of record deer harvested may represent areas where environmental characteristics promote record deer production and harvest. Although record deer harvested in the Driftless ecoregion possess antlers smaller than the average for the Midwest (Cain 2020 – Chapter 2), the number of record deer harvested was greatest in the Driftless ecoregion relative to other ecoregions in the Midwest. Conversely, areas with fewer harvests of record deer than expected may represent places where poorer quality habitats have resulted in fewer harvest opportunities. Moreover, hunters in the Central Appalachians, for example, may have fewer opportunities to harvest, less success at harvesting, or infrequent reporting of successful harvests when a record deer is present in the area (Appendix B). Therefore, the ecoregion effect may also represent sociological differences among the hunting community.

My results suggest that a record deer was more likely to be harvested and reported when at least one record deer was reported in the previous year. This could be a cultural artifact in that a hunter may be more likely to report a record deer in areas where record deer have been reported recently. Given the large amounts of private land in the Midwest, it is common for hunters to pay farmers and other landowners for access to their land for hunting opportunities (Hansen 2011, VerCauteren and Hygnstrom 2011). The landowner may charge any amount that they see fit, thus hunting leases vary in costs. In areas where hunters have the opportunity to harvest male deer with large antlers, hunting leases may be more expensive because the opportunity to hunt record deer seems to be important to hunters (Eliason 2008, Whittington 2014). Consequently, if hunters are concerned that reporting the harvest of a record deer will lead landowners to increase the cost of hunting leases in the area, then the hunter may decide not to report a record deer (Adams et al. 2011). Thus, positive temporal autocorrelation makes sense because hunters may be more likely to report a record deer when there was a record deer reported the year before.

My results suggest that implementing management strategies focused on the male segment of the population have the potential to influence record deer harvests in the area. First, the number of record deer was greater in counties that had antler point restrictions (1.5 deer/year) compared to the harvest in counties that did not have these regulations (1 deer/year). Management regulations restricting the harvest of yearling males, such as antler point restrictions, increase the probability that they will survive the hunting season and reach older ages. Previous research shows that antler point restrictions protect sub adult males from harvest with a greater proportion of the male harvest consisting of individuals from older age classes (Hansen et al. 2017, Wallingford et al. 2017, Cain 2020 – Chapter 1). Antler size increases with the age of the individual (Demarais and Strickland 2011), and counties with antler point restrictions have experienced greater harvests of adult males with larger antlers (Wallingford et al. 2017).

Second, limiting the number of antlered deer that hunters could harvest per year had a positive influence on the number of record deer. Implementing a limit on buck harvest decreases the overall harvest of male deer, which increases the number of males that survive the hunting season. However, unlike antler point restrictions, limiting the number of bucks does not protect a certain age class. Hunters in the Midwest generally harvest 1–2 deer each year (VerCauteren and Hygnstrom 2011). The values derived from or assigned to a wildlife resource vary from person to person (Conover 1997), but hunters want an opportunity to hunt bucks every year (Cornicelli et al. 2011). By limiting hunters to 1 buck per year, hunters may become more selective in the buck they choose to harvest.

My results suggest a negative relationship between the number of record deer and the length of the hunting season. The harvest under 33-day hunting season (0.68 deer) was smaller than the expected harvest under a 6-day hunting season (1.76 deer). This finding makes sense given previous work showing that deer change their movement behaviors to minimize harvest risk during the hunting season (Whitman 2012, Little et al. 2014, Marantz et al. 2016). The vulnerability of deer to harvest is influenced by the habitat and deer movements (Whitman 2012). Alterations made to the length of the hunting season influence the activity and timing of hunters in the field, and deer respond rapidly to their presence by changing their movement to avoid harvest risk (Little et al. 2016, Marantz et al. 2016). Longer seasons afford hunters more opportunities to get out in the field by offering hunters more days doing so, but my results suggest that there is not necessarily a corresponding increase in harvests of record deer. This is likely due to the influence of hunting pressure on deer movements, which affects the vulnerability of deer to harvest (Whitman 2012).

Roseberry and Klimstra (1974) reported that hunters tend to select for adults over fawns and males over females when harvesting deer. Diekert et al. (2016) used ideas from economic search theory to describe an individual hunter’s decision to shoot a deer or not. There are fixed costs (e.g., license fees, lease payments, opportunity costs of traveling) associated with hunting and these investments made by the hunter influence their individual threshold value for choosing to shoot an animal. From the perspective of the hunter, any deer valued at or above the threshold are subject to hunting while animals valued below are safe from being shot. The higher the opportunity cost incurred by the hunter, the lower their reservations to harvesting the deer that they see (Diekert et al. 2016). The value of a deer is based on the hunter’s expectations of the herd, investments made by the individual (Diekert et al. 2016), and the relative importance the hunter places on various characteristics of the animal (e.g., antler size, sex, age). Therefore, similar to beauty, the value of the deer is in the eye of the beholder. The decision to shoot an animal is unique to the hunter, the value placed on the animal trait, and harvest restrictions and regulations (Mysterud 2011, Ramazin and Sturaro 2014).

As interest in quality deer management and harvesting adult males with large antlers increases (Connelly et al. 2012, Harper et al. 2012), it is important for wildlife managers and hunters to understand how regulations can influence harvests of record deer. Although research has been conducted on factors affecting antler growth and development (Demarais and Strickland 2011 and references therein), no studies have investigated the relationship between record deer and management regulations. My analysis demonstrates that changes in management regulations can influence the harvest of record deer in the Midwest with inherent differences among ecoregions. In areas of highly suitable habitat for white-tailed deer, management regulations, such as shorter season and limiting the harvest of antler deer, can provide enhancements to survival of antlered deer that may result in the additional harvest of record deer.

APPENDIX

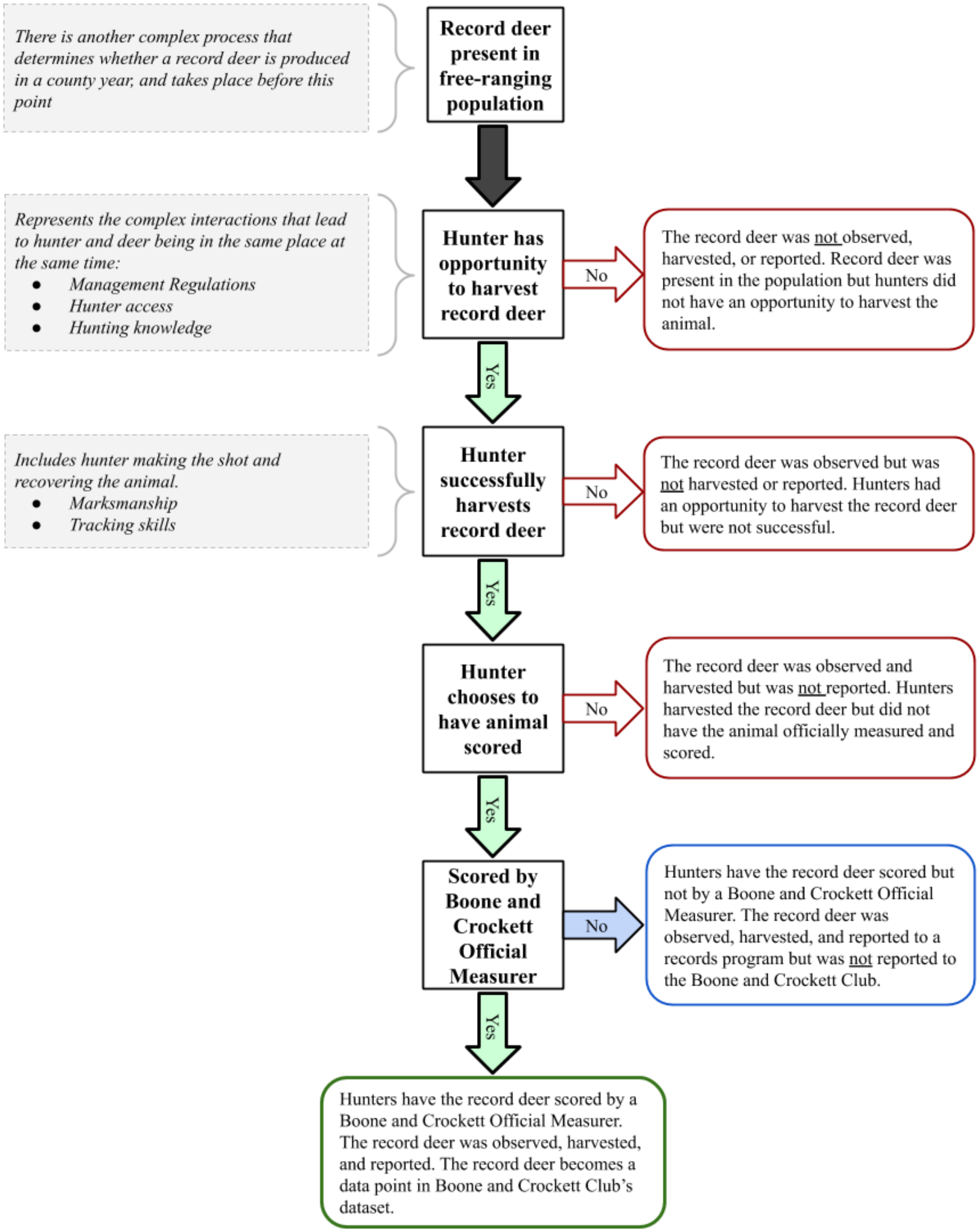

Figure 3.4 Infographic to show the sequence of critical steps required for a male white-tailed deer that has record-sized antlers to become a data point in the Boone and Crockett Club's Records of North American Big Game. Influential factors that may direct the outcome (Yes/No) of each step are given in the gray boxes.

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CHAPTER 4: ADDRESSING UNCERTAINTY IN THE REPORTING PROCESS OF THE BOONE AND CROCKETT RECORDS

INTRODUCTION

Quantifying the abundance and distribution of animals in a free-ranging population is one of the principal goals of wildlife research (Williams et al. 2002, Kellner and Swihart 2014). A major challenge in obtaining measures of abundance is that some individuals in the population may avoid detection (Link and Sauer 1997). Consequently, a complete count of every individual in a population is usually impossible (Dice 1941, Dénes et al. 2015), and monitoring is generally based on a subset of the total population. The probability that an animal is counted given its presence in the population is known as the detection probability (p, Williams 2001). Ecological models that use counts of individuals as proxies for abundance assume the detection probability is perfect ($p = 1$) or proportionally related to abundance by a constant (Williams 2001, Kéry et al. 2005). In most situations, species are imperfectly detected (i.e., detection probability < 1) and this assumption is violated (Ficetola et al. 2018). Similar to data collected from field observations, data collected from hunter harvest surveys are also subject to issues of imperfect detection (Rosenberry et al. 2004, Goddard and Miller 2009), because the probability that a hunter reports a successful harvest varies through time and across space (Roseberry and Woolf 1991, Rosenberry et al. 2004).

For game species, such as white-tailed deer (*Odocoileus virginianus*), harvest data represent an important source of information that are commonly used by managers to monitor trends in wildlife populations subjected to hunter harvest (Roseberry and Woolf 1991, Brown et al. 2000, Kilpatrick et al. 2005, Goddard and Miller 2009, Monteith et al. 2013). Estimating annual harvests of deer and inferences drawn about harvest trends are essential for informing and appraising management decisions (Rupp et al. 2000). Failing to account for variation in the detection probability (or reporting rate) in harvest data can lead to biased estimates and erroneous inferences about trends in harvest (Williams et al. 2002, Rosenberry et al. 2004, Fiske and Chandler 2011, Guillera-Arroita 2016).

Issues of imperfect detection, when in reference to harvest estimates, may be magnified when animals are rare leading to small sample sizes. The white-tailed deer recorded in the Boone and Crockett Club's Records of North American Big Game (hereafter referred to as record deer, Reneau et al. 2011) are examples of rare animals. Moreover, the record deer that are reported represent an unknown subset of white-tailed deer with large antlers harvested from a population. The Boone and Crockett Club does not solicit this information, but rather the process of entering a record deer is initiated by the individual hunter (Nesbitt and Wright 2016). An anticipated consequence of social, economic, or other types of barriers that impede a hunter from registering a harvested deer is that the animal is less likely to be reported. Therefore, analytical approaches using harvest data reported by hunters must account for imperfect detection to avoid inaccurate inferences about trends in record deer harvest (Mackenzie et al. 2005, Ryan et al. 2019).

One of the more recent developments in accounting for imperfect detection in abundance estimation is the N-mixture modeling framework (Royle 2004). This framework explicitly accounts for imperfect detection by using a hierarchical model to estimate parameters for abundance and detection probability from spatially and temporally replicated counts of unmarked individuals (Royle 2004). One level of the hierarchy serves to describe the variation in abundance, while another describes the observations conditional on the abundance (Royle and Dorazio 2008). A third level can be added to the hierarchical model to describe the suitability of sites, which is a useful extension when zero-inflation in the data is a concern (Kéry and Schaub 2012). The flexibility of this modeling framework allows the inclusions of covariates, which are linked through a generalized linear model link function, that are believed to influence population abundance, site suitability, or detection probability (Kéry and Schaub 2012).

Despite the flexibility inherent in the n-mixture modeling framework, no one has investigated the applicability of using this modeling framework to evaluate trends in harvest data. Therefore, in this chapter I seek to evaluate whether n-mixture models could be used to address concerns related to imperfect detection (or reporting rates) for harvest data. My goal is adapt the zero-inflated n-mixture modeling framework to model data on harvests of record deer in Wisconsin from 2 independent record keeping organizations (i.e., Boone and Crockett Club, Wisconsin Buck and Bear Club). My specific objective for this chapter were to: 1) determine if reporting rates (detection probabilities) show biases in space or time and 2) evaluate the influence of land cover and harvest characteristics on the harvest of record deer. Wisconsin provides a good place to look at the potential of applying this method because both sources of record deer data have been collecting for many years.

STUDY AREA

The study area consisted of 71 of the 72 counties in Wisconsin. I excluded Menominee County from this analysis because most of the county is under Menominee Tribal jurisdiction with deer hunting regulated by the Tribal government (Wisconsin Department of Natural Resources 2019). The advancing and retreating of glaciers across the Upper Midwest shaped the landscape of Wisconsin and fundamentally influenced development of ecosystems in the study area. The Driftless Area ecoregion (Bailey 1983, Bailey 1995) covers about 20% of Wisconsin, primarily along the Mississippi River, and denotes an area that escaped the most recent glaciation. Wisconsin is characterized by a mixture of agriculture and forested land. While agriculture occurs statewide, production is more dominant in the southern portion of the state (Wisconsin Department of Natural Resources 2012). The most extensive deciduous forests are found in Northcentral Wisconsin (Wisconsin Department of Natural Resources 2012).

During the years of my analysis, the Wisconsin Department of Natural Resources modified some of the regulations for hunting white-tailed deer in the state, including implementing Earn-A-Buck (EAB) regulations intending to increase antlerless harvest, and subsequently decrease population growth rate (McCullough 1984). An annual limit of 2 bucks was imposed on all hunters in Wisconsin for the duration of this study.

METHODS

Observed Data – Independent Counts of Record Deer

For my response variable in this chapter, I obtained records of white-tailed deer for 1981–2014 from 2 independent record-keeping organizations: the Boone and Crockett Club and the Wisconsin Buck and Bear Club (WBBC). The timeframe was determined by data availability, and 1981 was the first year that population estimates and detailed summaries of season frameworks were available for each deer management unit (personal communication; Robert Rolley, Population Ecologist for the Wisconsin Department of Natural Resources).

The Boone and Crockett Club established a standardized system for measuring and scoring big game in North America and maintained the data to serve as a baseline for future studies that investigate trends in record animals (Nesbit and Wright 2016). The system was designed to emphasize bilateral symmetry by penalizing the final score based on the amount of asymmetry; detailed measurements of antler characteristics and specific calculations produce a numerical final score that serves to rank the animals of a particular category (Reneau et al. 2011). All measurements are the same between typical deer and nontypical deer; however, the 2 categories differ in how they incorporate abnormal points into the final score (Nesbit and Wright 2016). To be entered into the Boone and Crockett records, the animal must be scored by an Official Measurer that was trained by the Club. In addition to the scoring details (e.g., individual measurements, calculated scores), each entry included the county of harvest and the year it was taken. I organized my observed count data using this information on the location and year of harvest.

The WBBC began in 1965 to enhance the information on the harvest of record deer in Wisconsin (WBBC 2019). While the WBBC adheres to the same scoring system as Boone and Crockett, they have their own measurers. That said, 31 (55.4%, Wisconsin Buck and Bear Club 2020) of the state certified official measures are also Boone and Crockett official measures, but not all. Volunteers for the WBBC travel across the state and attend different sporting shows to measure harvested animals. Although the Wisconsin Buck and Bear Club has a lower minimum entry score, I limited the data to those records that met or exceeded the minimum score required by the Boone and Crockett Club (406.4 cm for typical and 469.9 cm for nontypical). This cut off ensured that I did not count any records that would not qualify for entry in the Boone and Crockett Club records. For each county and year, I used the data sets to produce two independent counts of record deer from the same population.

Model Covariates

To evaluate the influence of land cover on the harvest of record deer, I used ArcGIS (version 10.1; Environmental Systems Research Institute, Redlands, California, USA) to reclassify the 2001, 2006, and 2011 National Land Cover Database (Fry et al. 2011) to correspond to important land cover for white-tailed deer (Alverson et al. 1988, Williams et al. 2012, Dechen Quinn et al. 2013, Snow et al. 2018, Cain et al. 2019). I used the reclassified data and program FRAGSTATS (version 4.1, University of Massachusetts, Amherst, Massachusetts, USA) to calculate 2 landscape metrics meaningful to deer in each county (i.e., contrast weighted edge density [CWED] and percentage of agriculture [AG_LAND]). CWED represented the sum of the borders between cover types multiplied by a corresponding contrast-weight (i.e., weight = 1 for agriculture and forest cover types, and weight = 0 for all other cover types) divided by the area of the county (km/km^2). AG_LAND denoted the percentage of the area within a county that was classified as agriculture cover.

Before a deer on the landscape can be entered as a record deer, it must first be successfully harvested (Appendix D). The vulnerability of antlered deer to harvest is influenced by hunting regulations, environmental conditions, and the behavior and density of deer and hunters (Roseberry and Klimstra 1974, Roseberry and Woolf 1998, Brown et al. 2000, Stewart et al. 2011). The Wisconsin Department of Natural Resources provided annual harvest data for antlered white-tailed deer. To evaluate the influence of harvest characteristics on the harvest of record deer, I calculated the total number of antlered deer taken in each county for the year (ANTLERED) by adding together the number of antlered deer harvested across all the hunting seasons (e.g., archery, crossbow, gun) from 1981–2014. I evaluated collinearity in my covariates by assessing if the values were correlated ($|r| < 0.6$).

The Institutional Animal Care and Use Committee at Michigan State University determined that the acquisition of harvest data from the Boone and Crockett Club, Wisconsin Buck and Bear Club, and Wisconsin Department of Natural Resources was exempt from protocols by the Animal Care and Use Committee. I followed guidelines outlined by the Boone and Crockett Club and Wisconsin Buck and Bear Club for securely processing and storing the data supplied for this research.

Modeling Framework

I setup the model to allow the probability of detecting a record deer to vary across space and over time. I used a zero-inflated Poisson N-mixture modeling framework to develop a hierarchical model to estimate the number of record deer harvested in each county (Appendix A). I estimate county-level detection probabilities for record deer by treating the Boone and Crockett and WBBC records as independent double count data. I modeled the observation process as:

$$y_{i,j,k}|N_{i,k} \sim Binomial(N_{i,k}, p_{i,k}),$$

where $y_{i,j,k}$ was the total count for each sampling unit (i.e., county) i $(i = 1 \dots 71)$ during replicate j $(j = 1, 2)$ and year k $(k = 1 \dots 34)$. This binomial process rendered the identification of individuals irrelevant because the detections of record deer were random events (Royle and Dorazio 2008). $N_{i,k}$ was the parameter representing the estimated number of record deer after correcting for imperfect detection. The harvest of record deer in county i during a given year k was the outcome of a latent process, because it cannot be directly observed in the data (Royle et al. 2005, Kéry and Schmidt 2008).

Given how the harvest of a record deer is a rare event, the data exhibit an excessively greater number of zero-counts than would be expected from a Poisson distribution.

Consequently, each county is more likely to have a value of zero than any other number. Therefore, I included an additional hierarchical level that characterized the suitability of a county for record deer that was able to deal with the excess zero-counts as part of a Bernoulli distribution process (Kéry and Schaub 2012). This binary level of the hierarchical model was:

$$z_{i,k} \sim Bernoulli(\Omega).$$

A uniform distribution was used as an uninformative prior for the proportion of suitable sites Ω, because parameter Ω could only take on values between 0 and 1 (Link and Barker 2010). The site suitability $z_{i,k}$ followed a Bernoulli random distribution with probability Ω. It was necessary to include this additional hierarchical level in the model, because the zeros could represent either a void of record deer harvested in the county (e.g., true zeros, unsuitable sites) or an omission of record deer that were harvested successfully but never reported (e.g., false zeros, reporting bias). Given that a county was suitable (i.e., when $z_{i,k} = 1$), the estimated number of record deer harvested was modeled following a Poisson process:

$$N_{i,k} | z_{i,k} \sim Poisson\ (z_{i,k} * \lambda_{i,k}),$$

where the $N_{i,k}$ is the true harvest for county *i* during year *k*. The $\lambda_{i,k}$ is an intensity parameter, which is conditioned on covariates, for county *i* and year *k* and modeled as:

$$\log(\lambda_{i,k}) = \alpha_k + \beta_k * X_{i,k},$$

where the α_k is the intercept and β_k is the slope that quantifies the log-linear relationship between lambda and covariates $X_{i,k}$. For this analysis, I included the AG_LAND, CWED, and ANTLERED in each county as independent covariates to estimate the true harvest of record deer for each county and year. I chose these covariates because of their influences on antler sizes of male deer and on the vulnerability of white-tailed deer to harvest.

I used a Bayesian framework to estimate parameters for the N-mixture model using software program JAGS (Plummer 2003) in program R (R Core Team 2019). I assumed vague prior distributions for estimated parameters and used R package *jagsUI* (version 1.5.0) to streamline the analysis. I evaluated posterior distributions, MCMC trace plots, and $\hat{R}$ values for model convergence.

RESULTS

From 1981 to 2014, there were 1,350 records for white-tailed deer in the Boone and Crockett Club's Records of North American Big Game. After truncating the data for white-tailed deer based on the minimum score set by the Boone and Crockett Club, I included 3,679 records reported to the WBBC.

The N-mixture model performed well with $\hat{R}$ values below 1.1 for all years and counties (Gelman and Rubin 1992). My model demonstrated successful convergence of all parameters in a model that used an uninformative prior for detection. There was adequate mixing and convergence of parameters with visual inspection of the trace plots (see Appendix B; Gelman and Rubin 1992, Link and Barker 2010). My results show spatial and temporal variability in the detection (Figure 4.1, Figure 4.2). The mean detection probability (Figure 4.1) as determined by the posterior distribution was highest for Dodge County (0.55, CI: 0.15–0.93) and Buffalo County (0.55, CI: 0.31–0.78), whereas the smallest mean detection probability was found in Richland County, Wisconsin (0.30, CI: 0.06–0.72). Although the detection probabilities of each county vary across Wisconsin (Figure 4.1), there was no indication of spatial clustering; instead, the mean detection probability appeared to vary randomly across Wisconsin, with an average detection of 0.43 (range: 0.30–0.55). Similarly, the detection probabilities of the counties displayed no notable patterns in values through time (Figure 4.2).

The mean harvest of record deer was highest for Buffalo County (12.50 deer/year, CI: 10.41–16.85 deer/year) and lowest for Calumet County (0.80 deer/year, CI: 0.24–3.21 deer/year). Unlike, the distribution of detection probability values, the mean estimates for the true harvest of record deer appeared spatially distributed across Wisconsin (Figure 4.3). The number of record deer harvested across Wisconsin averaged 3.07 deer/year (range: 0.81–12.50). There was variation in the estimated number of record deer across the state (Figure 4.4). Dodge County, Wisconsin had the lowest amount of variation on average with a standard deviation of 0.73, while Crawford County showed the greatest variation in the estimated number of record deer with a standard deviation of 5.36 (Figure 4.4).

None of the covariates (i.e., AG_LAND, CWED, ANTLERED) that I included in the model had a significant influence on the number of record deer during every year of this study (Figure 4.5, Figure 4.6, Figure 4.7). Of the three covariates used to model the true harvest of record deer, only CWED was influential to the harvest of record deer for the majority of years. The posterior distribution for CWED showed that the influence CWED on the harvest of record deer was significant during 26 years (76.5%) of the study (Figure 4.6). Therefore, my results suggest CWED has a positive effect on the presence of record deer.

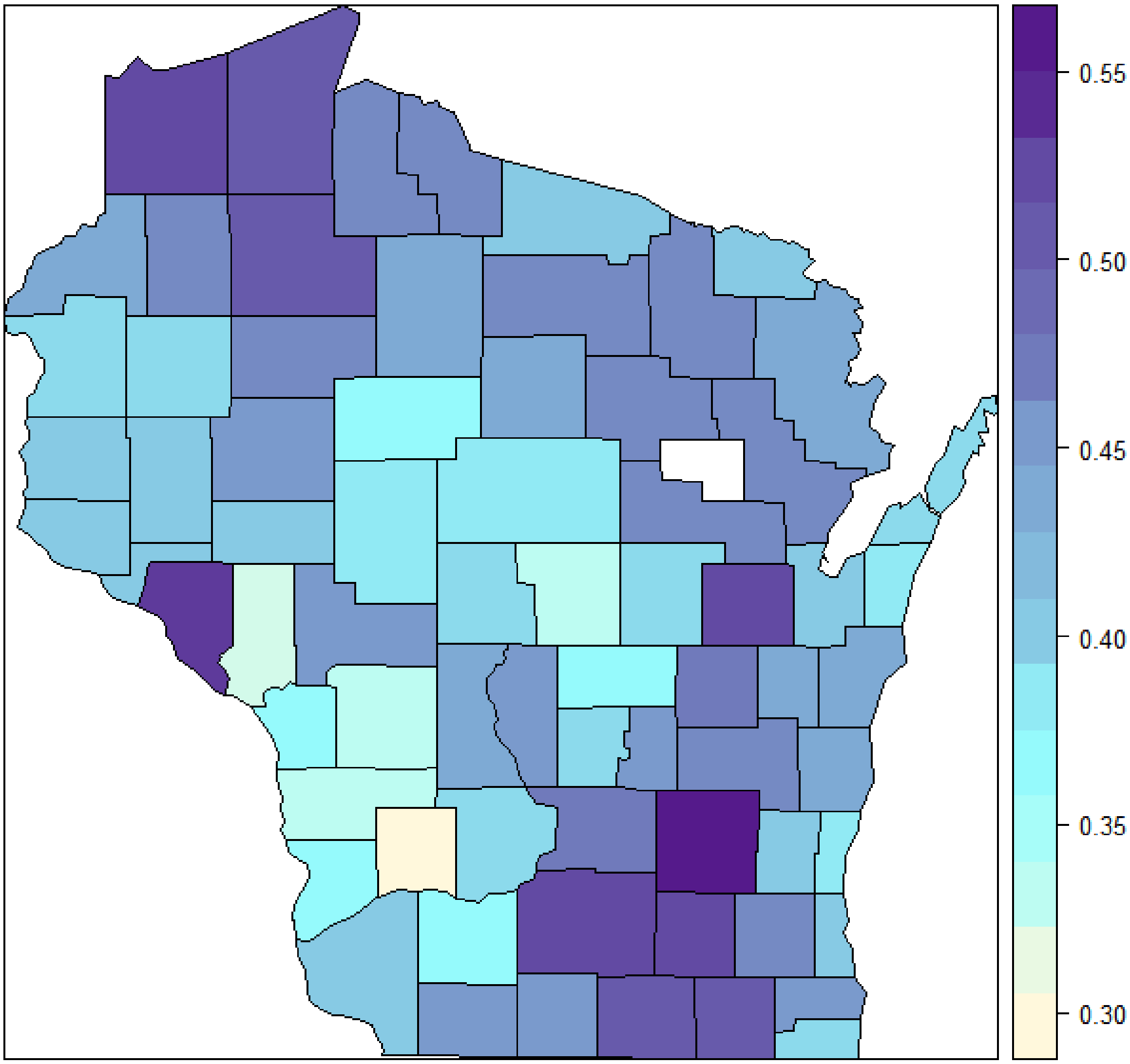


Figure 4.1 The mean detection probability for each county in Wisconsin from 1981–2014 estimated from the N-mixture model.

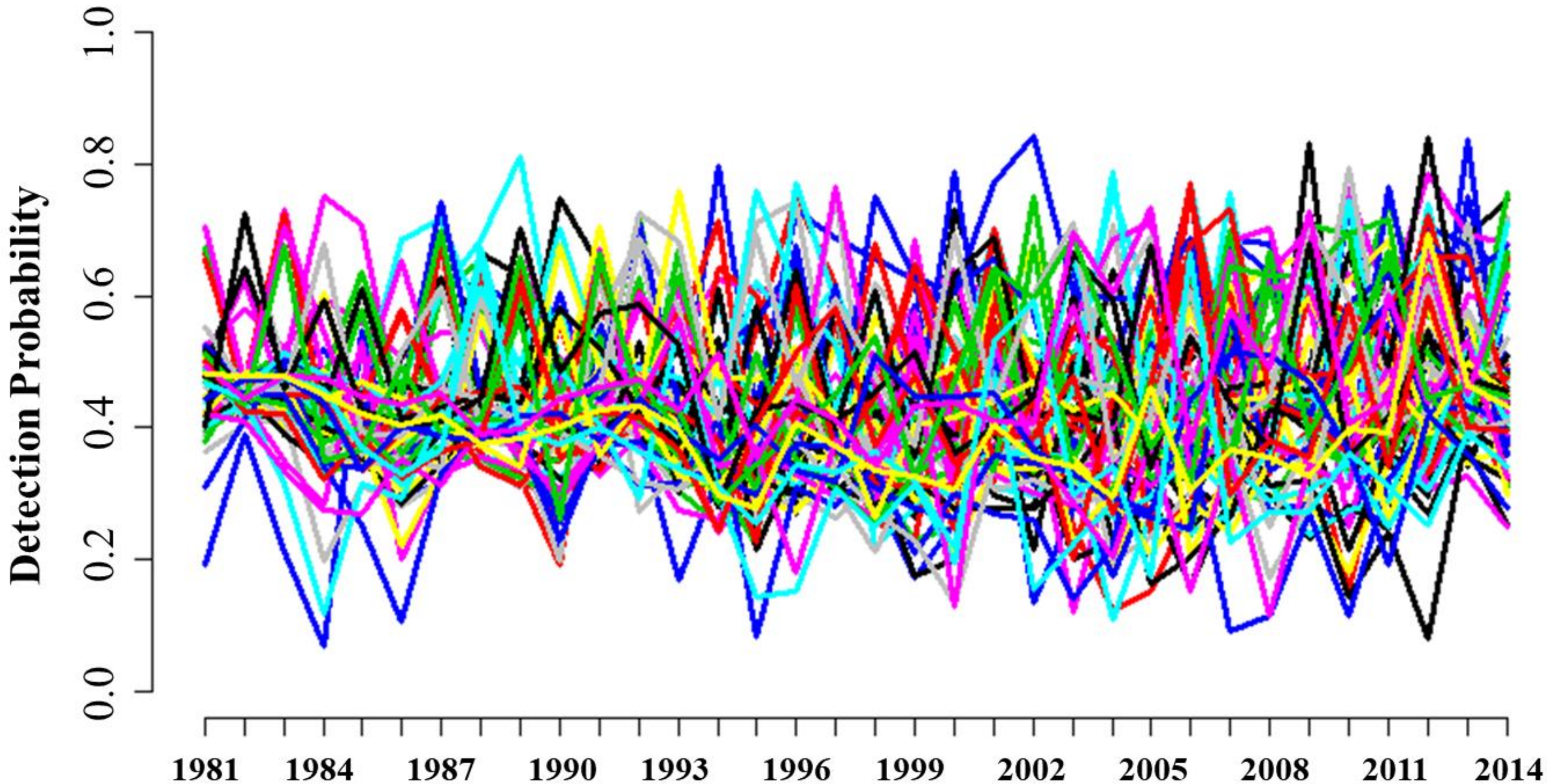


Figure 4.2 Detection probability of each county in Wisconsin from 1981–2014. Each line represents the detection probability for a single county through time.

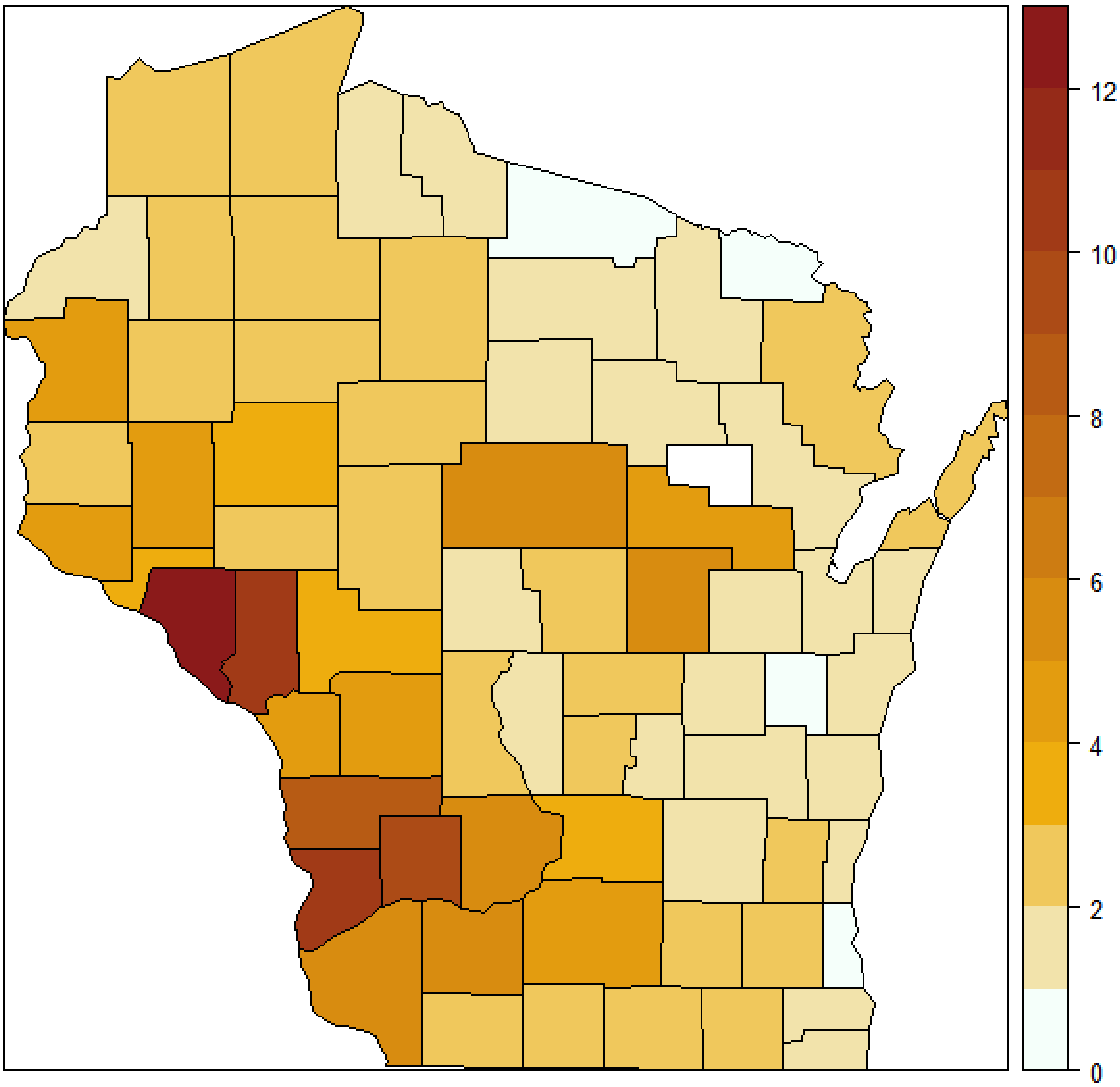


Figure 4.3 Mean number of record deer harvested from 1981–2014 in each county of Wisconsin estimated using the N-mixture model.

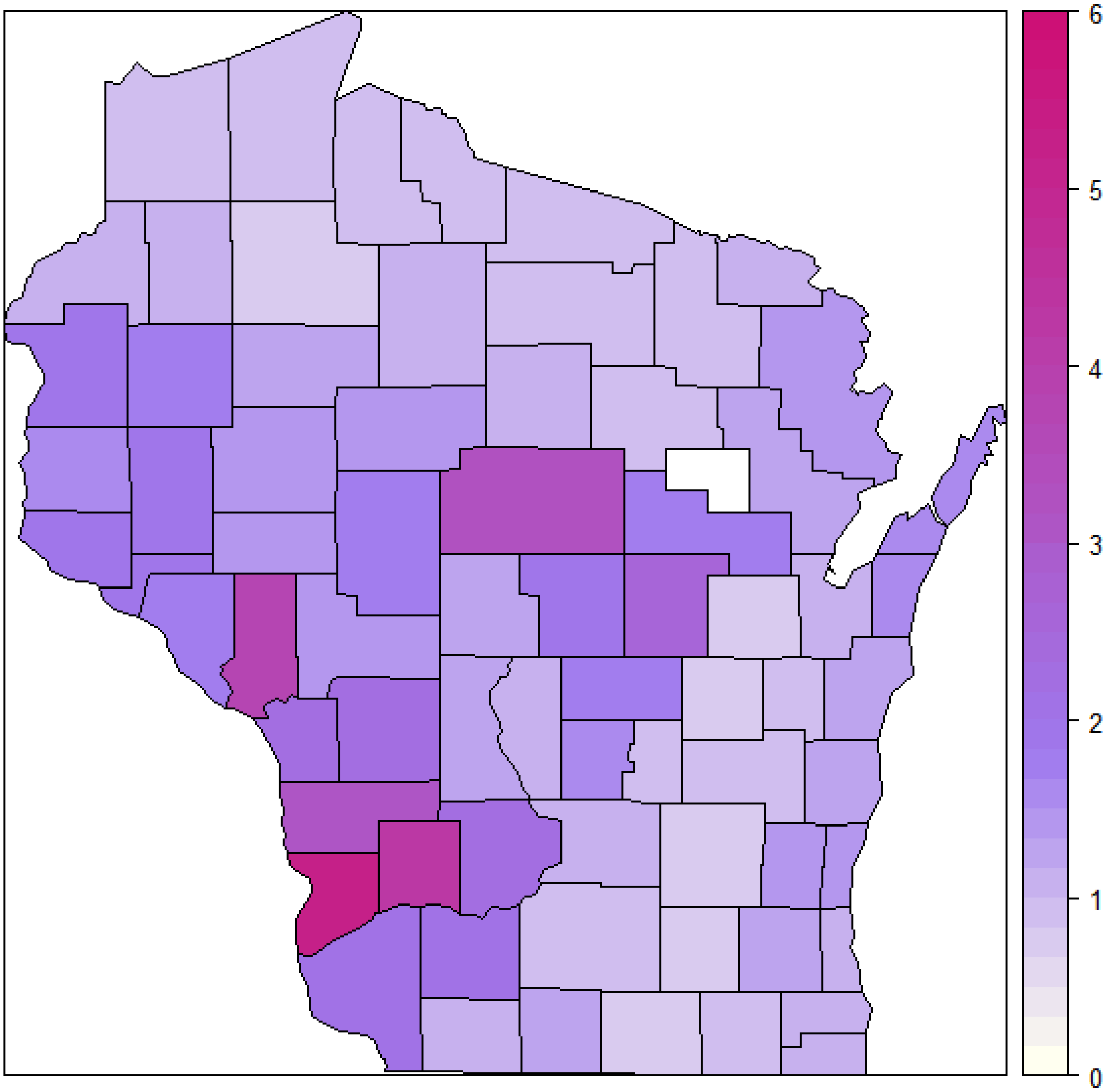


Figure 4.4 The standard deviation in number of record deer harvested estimates for each county in Wisconsin from 1981–2014 estimated from the N-mixture model.

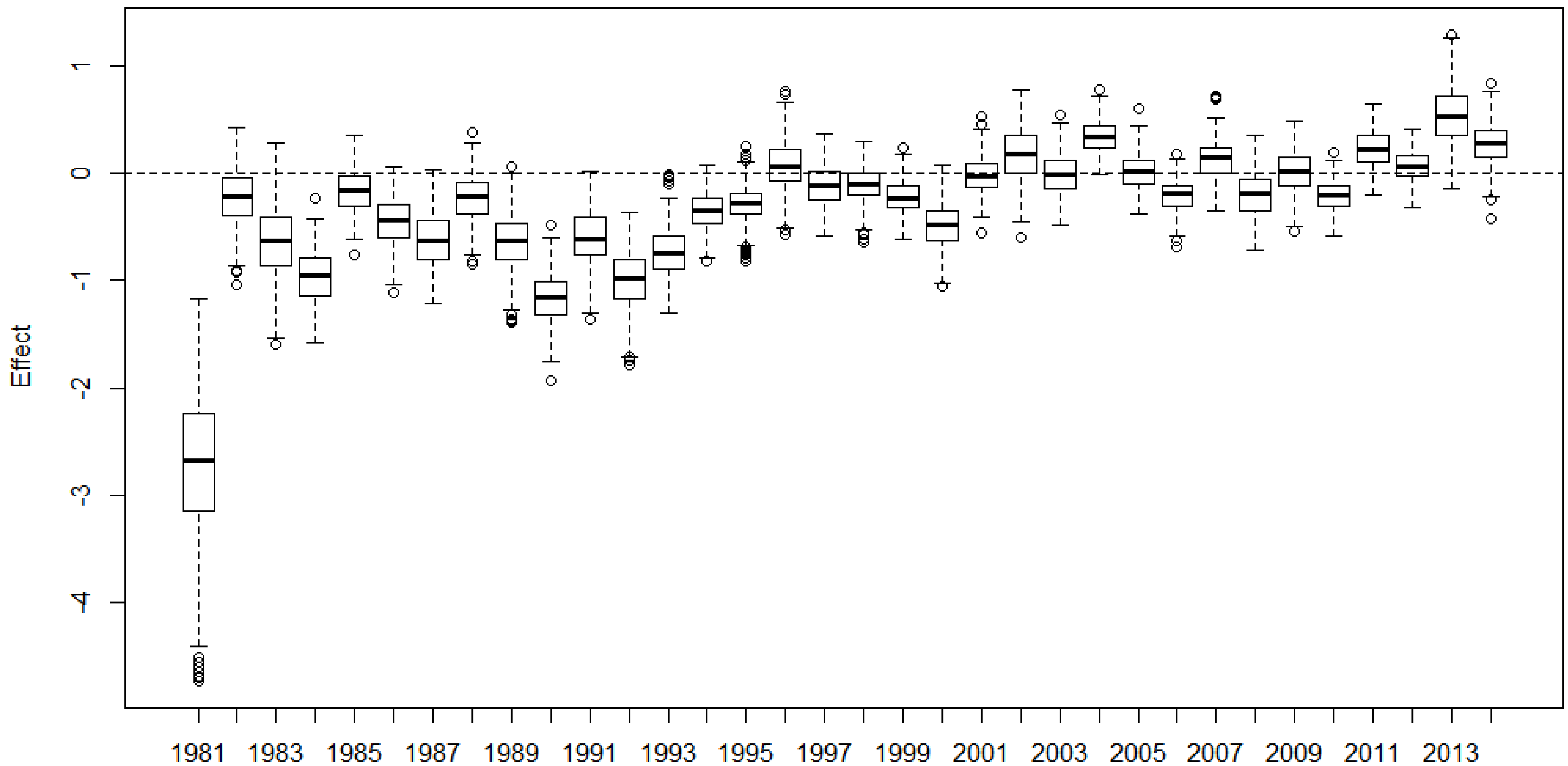


Figure 4.5 Posterior distribution of percent agriculture through time (1981–2014) in Wisconsin.

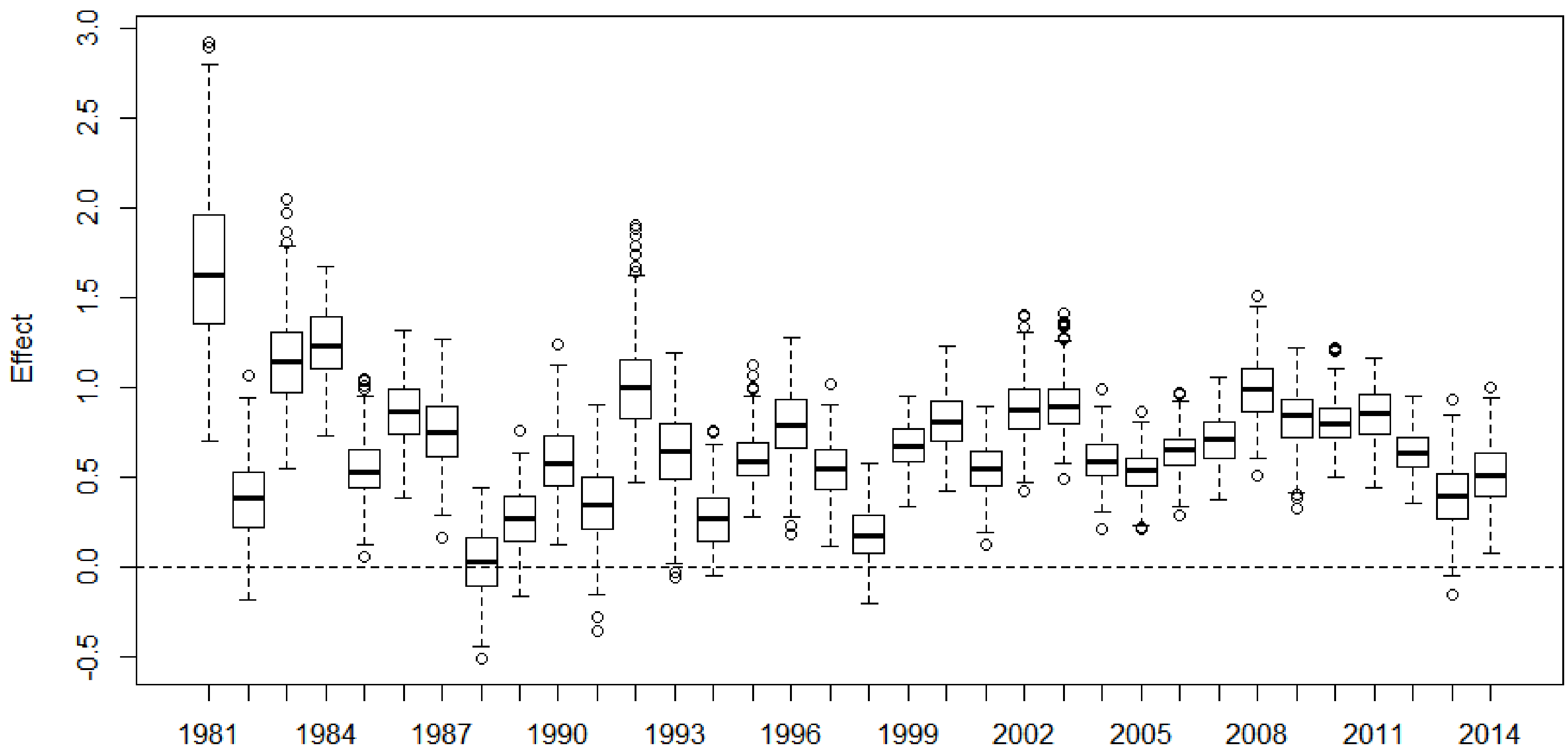


Figure 4.6 Posterior distribution of the Contrast Weighted Edge Density (CWED) metric to evaluate the influence of landscape configuration on the number of record deer harvested through time (1981–2014) in Wisconsin.

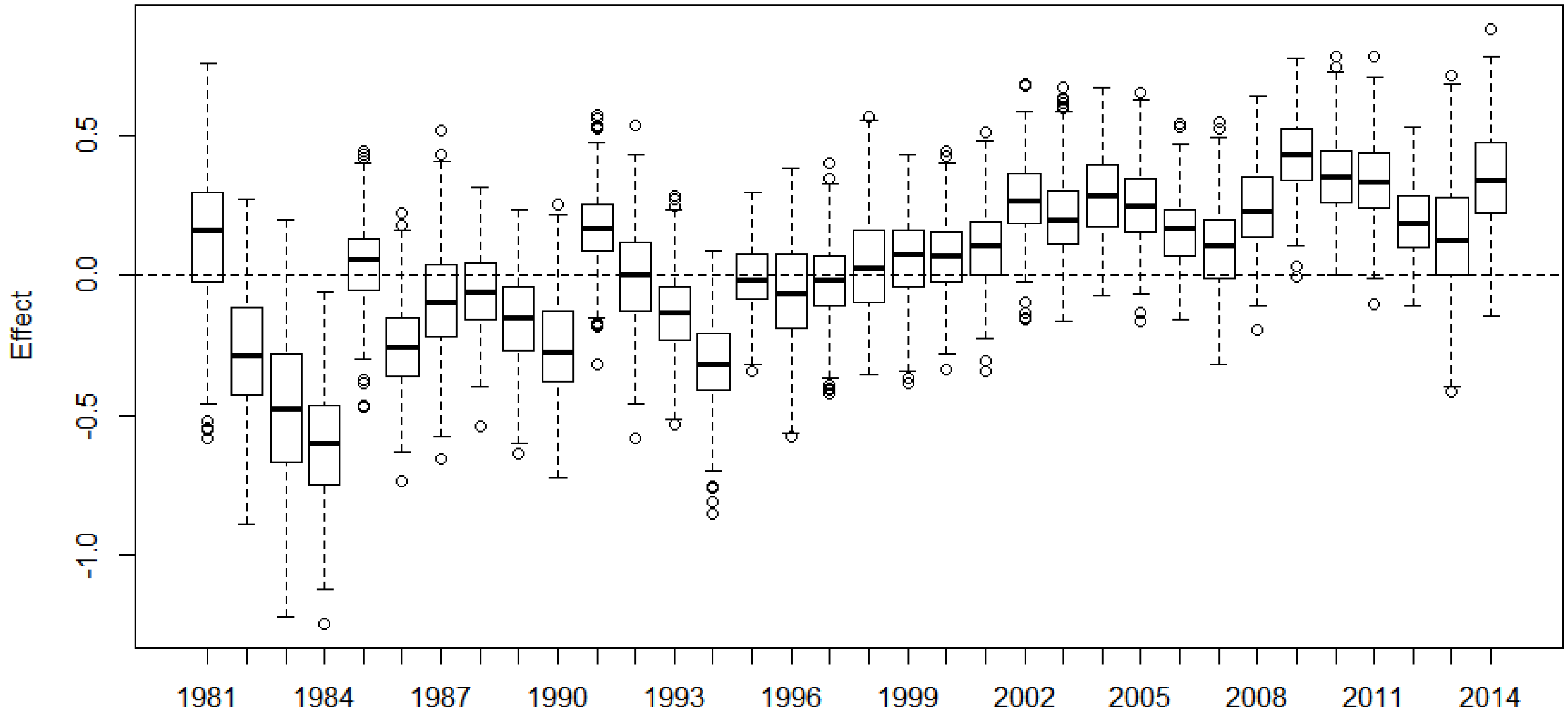


Figure 4.7 Posterior distribution of antlered harvest through time (1981–2014) in Wisconsin.

DISCUSSION

My findings provide a methodological proof of concept using the N-mixture modeling framework (Royle 2004) to estimate the number of record deer harvested with 2 independent sources of data. My results showed that detection probabilities do not appear to follow obvious spatial or temporal patterns, and randomness of detection suggests that factors related to detection of record deer are not influential. By using the N-mixture modeling framework to investigate record deer harvests, I was able to evaluate factors influencing trends in the harvest of record deer. I found that the number of record deer harvested was positively influenced by the CWED metric during most years covered in this analysis.

My study is the first application of the N-mixture modeling framework to generate detection corrected estimates of harvest from voluntarily reported harvest data. Traditional applications of N-mixture models have used data from repeated counts of animals observed on the landscape to estimate population abundance (Kéry et al. 2005, Keever et al. 2017, Christensen 2018). The detectability of individual animals is important to consider when estimating harvest of record deer because animals are detected (or reported) imperfectly. Researchers have long recognized that imperfect detection is pervasive in wildlife data, and limits our ability to draw conclusions from analyses (Williams 2001). While analysis does not get at the likelihood of an individual hunter deciding to report, the analysis does quantify the probability that the record deer is detected by the records. Moreover, my findings that the detection probability values vary randomly across time and space provide evidence that biases associated with reporting rates of record deer are random.

Multiple independent observations are required for the N-mixture modeling approach to be successful (Royle 2004). For my analysis of record deer, the multiple observations were count data from the Boone and Crockett Club and the Wisconsin Buck and Bear Club. One of the challenges remaining with the approach is that state-record programs do not exist for every state. Without this information, we cannot implement the N-mixture modeling framework to estimate harvests of record deer in states where these record programs do not exist. The difference in the number of records, with WBBC having more records than Boone and Crockett, was expected. WBBC actively seeks animals for their record book, and the Boone and Crockett Club relies on hunters to initiate the process for submitting a record deer.

The spatial distribution of record deer may serve as an indicator of high-quality deer habitat because large antler sizes are associated with deer in good condition (Ditchkoff et al. 2001). The southwestern portion of the state appears to have higher harvests of record deer on average (Figure 4.3). These counties are within and adjacent to the Driftless Area ecoregion (Appendix C), suggesting that the ecological characteristics that define Driftless Area influenced the harvest of record deer.

N-mixture models can provide new information about how a covariate influences the response through time. To illustrate this point, my results showed that none of the covariates (i.e., AG_LAND, CWED, ANTLERED) included in the model influenced the number of record deer during every year of this study (Figure 4.5, Figure 4.6, Figure 4.7). Therefore, not only was I able to quantify the effects of each habitat covariate for the entire timeframe, I could also evaluate how the effect has changed over the years. Habitat quality influences a variety of demographic and behavioral characteristics in cervids, including survival and recruitment (Ginnett and Young 2000, Hurley et al. 2014), body mass and condition (Strickland et al. 2001, Pettorelli et al. 2002), and timing of seasonal migration (Mysterud et al. 2017). Given the temporal nature of these dynamics, changes in the effect of habitat over time maybe of greater interpretative value than the average influence of habitat across the years of study.

My finding that CWED was positively associated with the number of record deer aligns with current understanding of deer ecology, because a mixture of agriculture and forested lands (VerCauteren and Hygnstrom 2011) is excellent habitat for an edge species like white-tailed deer (Alverson et al. 1988). High CWED values indicate areas with greater interspersion of the high-quality forage and cover types that are preferred by white-tailed deer (Roseberry and Woolf 1998, Walter et al. 2009, Dechen Quinn et al. 2013). Moreover, my results align with previous research from Cain et al. (2019). They analyzed data of record deer harvested from 9 states of Midwestern United States and found that more record deer were harvested in counties with greater amounts of high-contrast edges.

From this application of the N-mixture modeling framework, I found that the issues of reporting bias in analyses using harvests of record deer might not be as concerning as I expected. Instead, my results suggest that reporting rates vary randomly across space and do not follow any obvious temporal trends. Given our limited knowledge on the factors influencing the reporting rates of harvested deer, the N-mixture modeling framework is a good path forward for analyses using harvest data. The framework is flexible enough to allow the detection to vary (Royle 2004) and general enough that successful convergence of all parameters in a model that used an uninformative prior for detection was possible. Moreover, analyzing harvest data under the N-mixture modeling framework may provide new opportunities to understand the functional relationships between deer harvests and environmental covariates. This modeling framework might be successfully applied to other collections of harvest data that have information spanning multiple decades and large areas to explore relationships between harvests of the species and ecological patterns that have changed through time.

APPENDICES

APPENDIX A: ZERO-INFLATED POISSON N-MIXTURE MODEL

$$z_{i,k} \sim Bernoulli(\Omega)$$

$$N_{i,k}|z_{i,k} \sim Poisson\ (z_{i,k} * \lambda_{i,k}),$$

$$\log(\lambda_{i,k}) = \alpha_k + \beta_{AG\_LAND} * AG\_LAND_{i,k} + \beta_{CWED} * CWED_{i,k} + \beta_{ANTLERED} * ANTLERED_{i,k}$$

$$y_{i,j,k}|N_{,i,k} \sim Binomial(N_{i,k}, p_{i,k}),$$

APPENDIX B: TRACE PLOTS FOR PARAMETERS OF N-MIXTURE MODEL

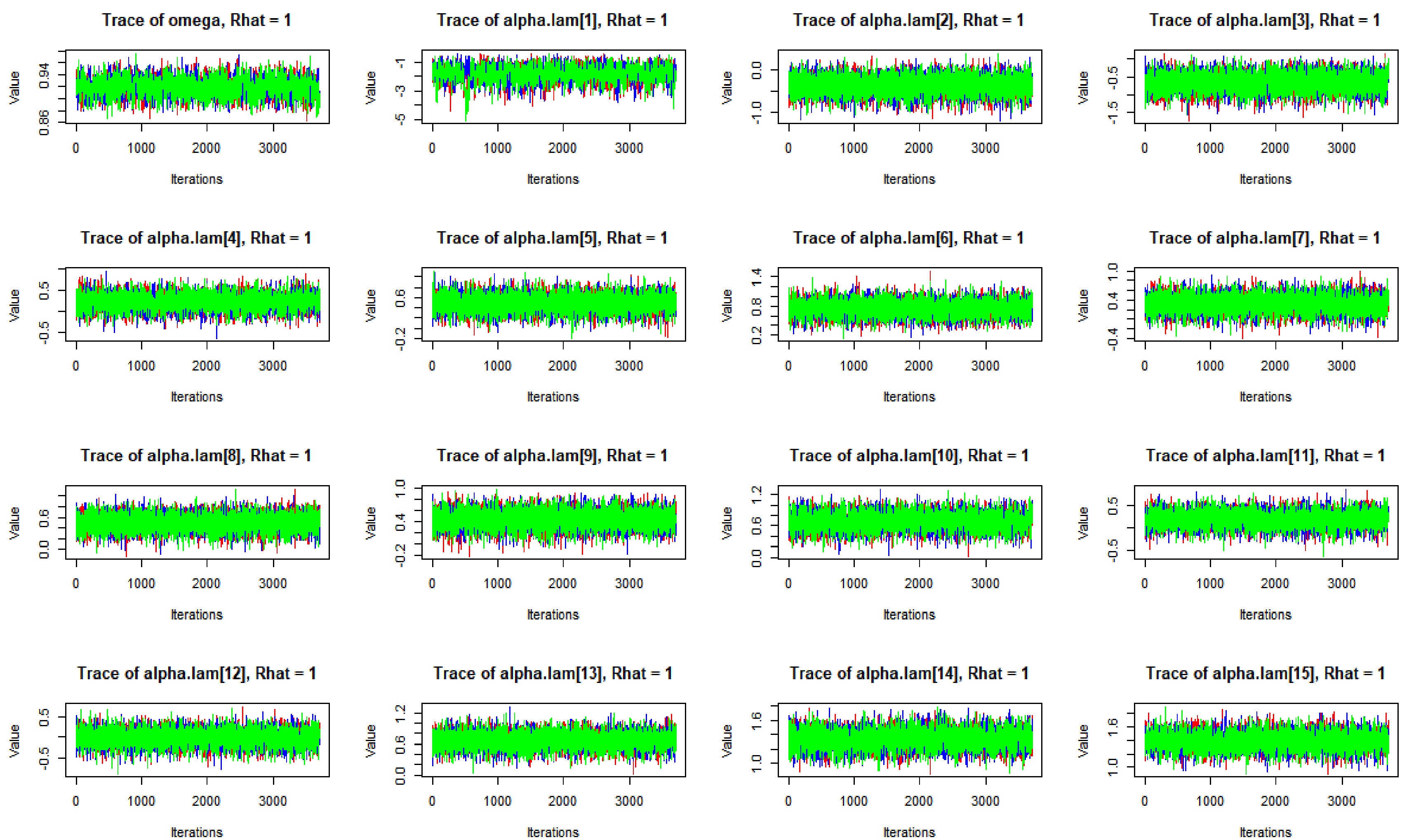
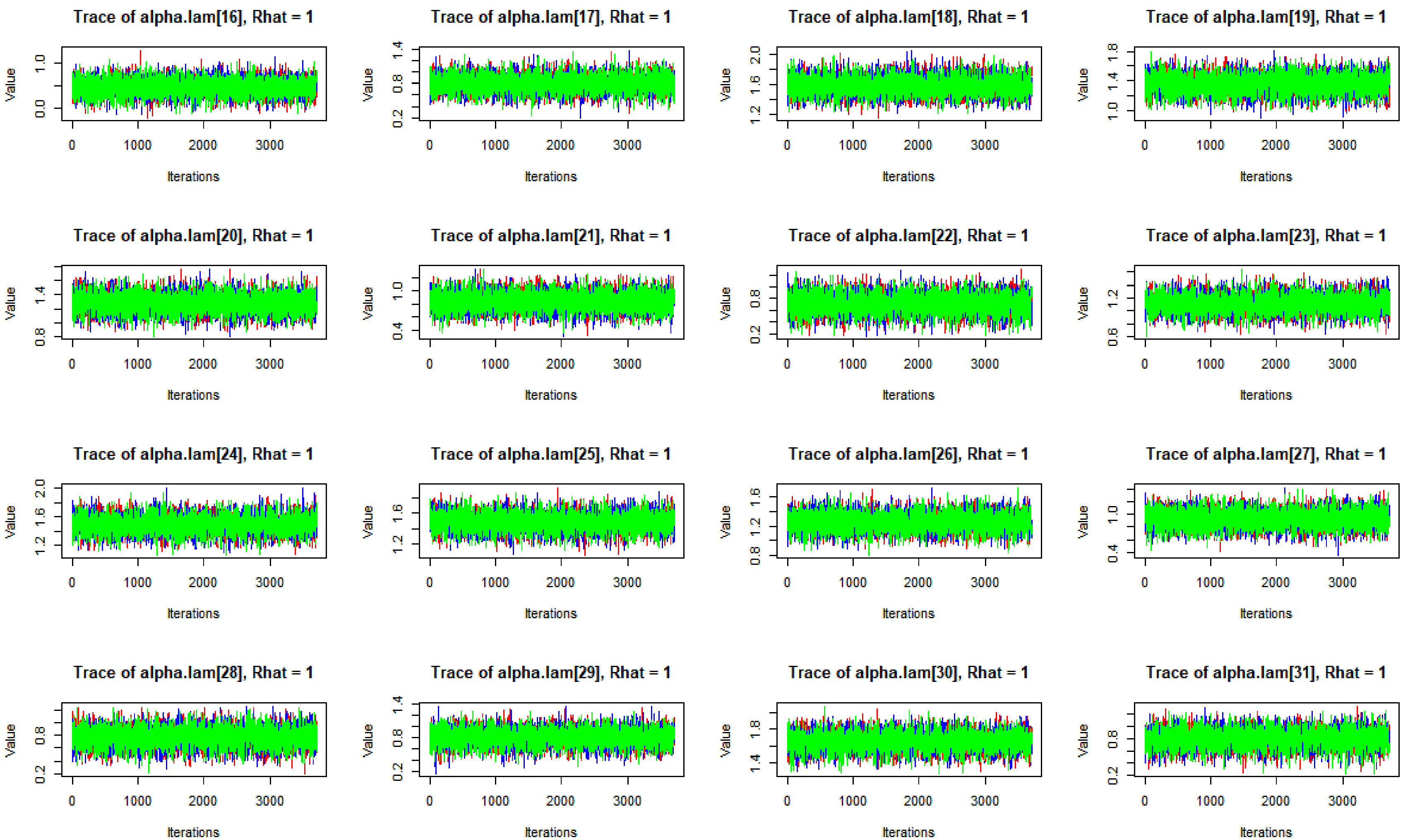


Figure 4.8 Trace plots of the values generated from the N-mixture model in Chapter 4 with the value of sample from MCMC process (y-axis) versus the iteration number (x-axis). Each plot represents the sampling histories of a single model parameter. These plots show that the chains for each parameter are mixing well over the parameter space.

Figure 4.8 (con’t)



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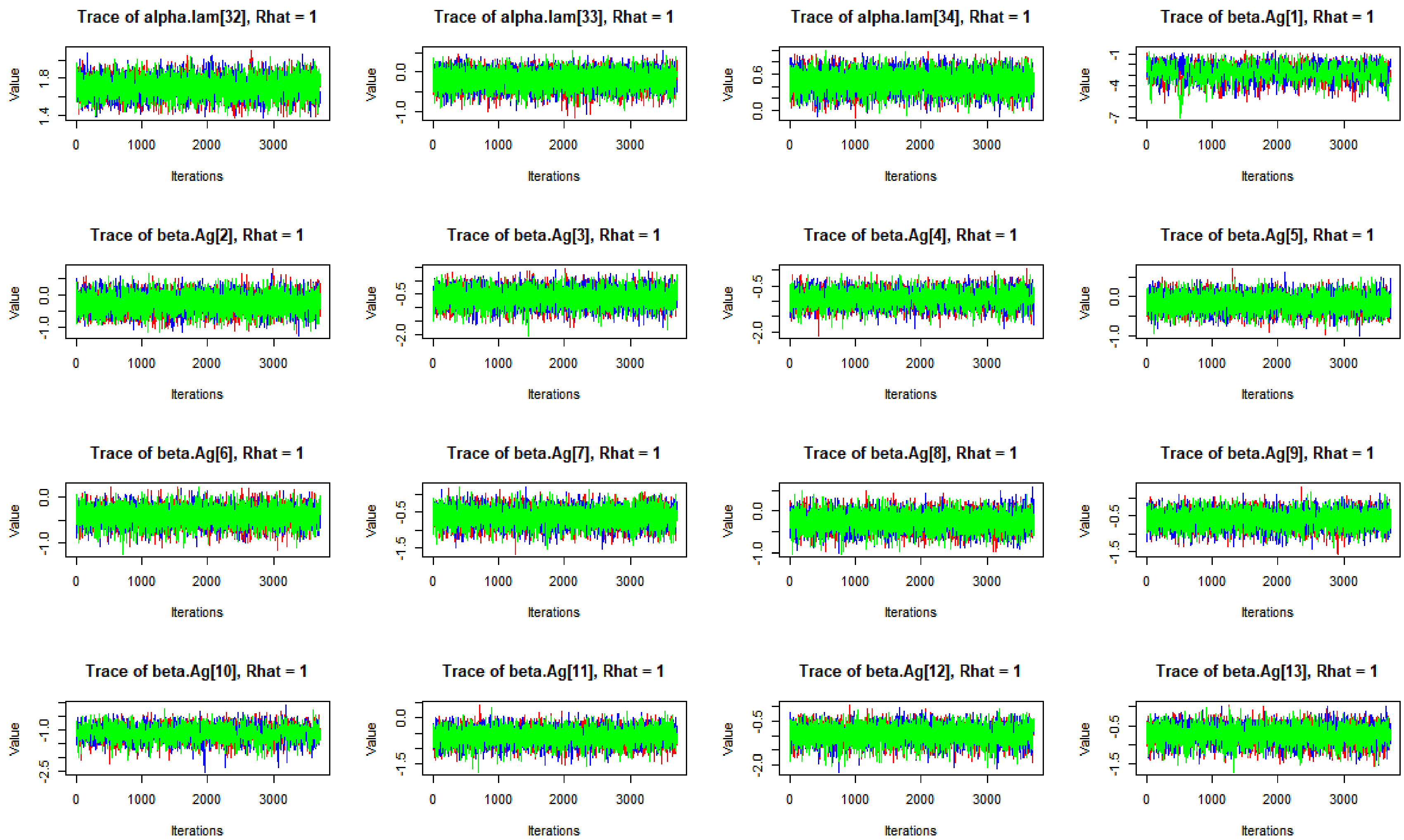

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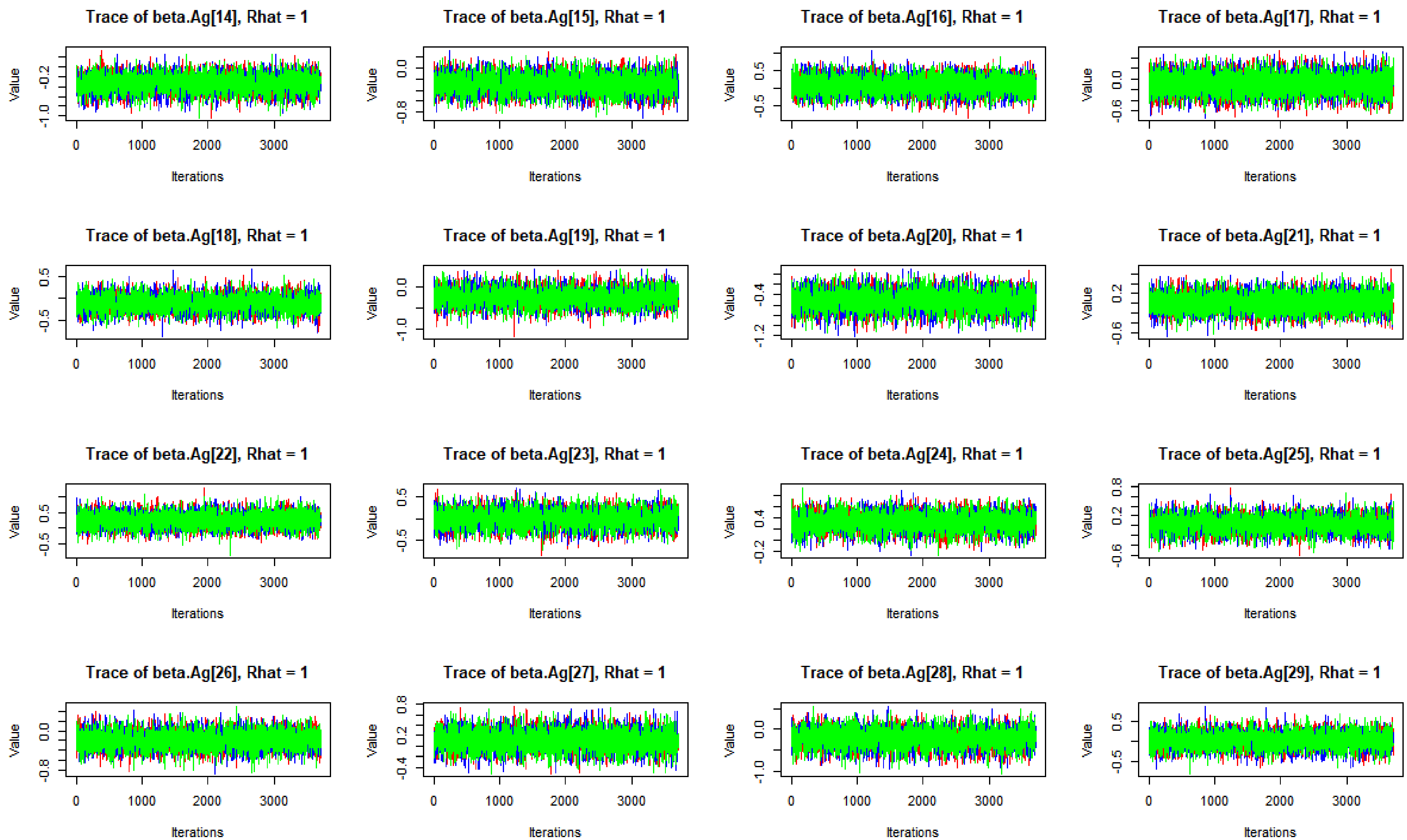

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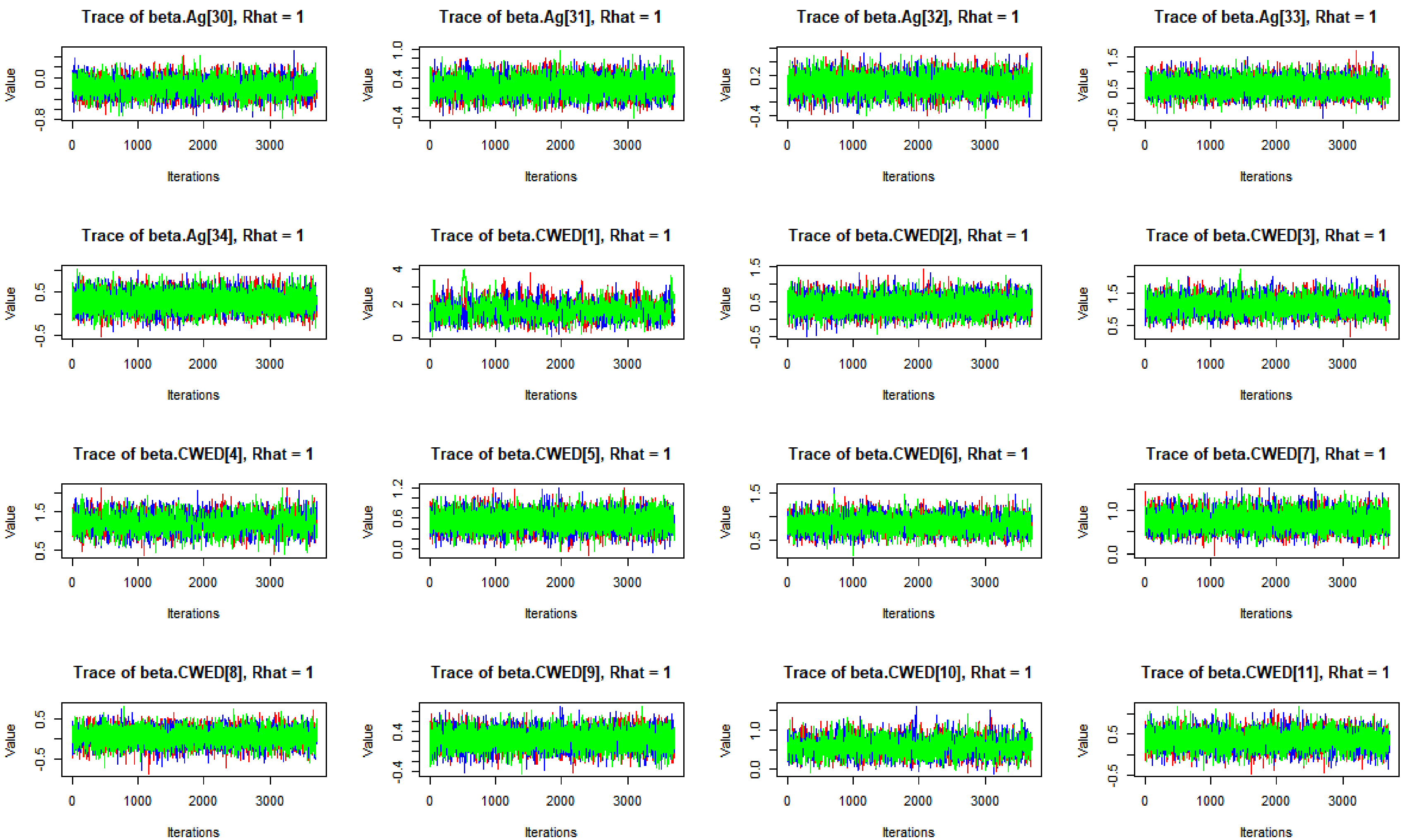

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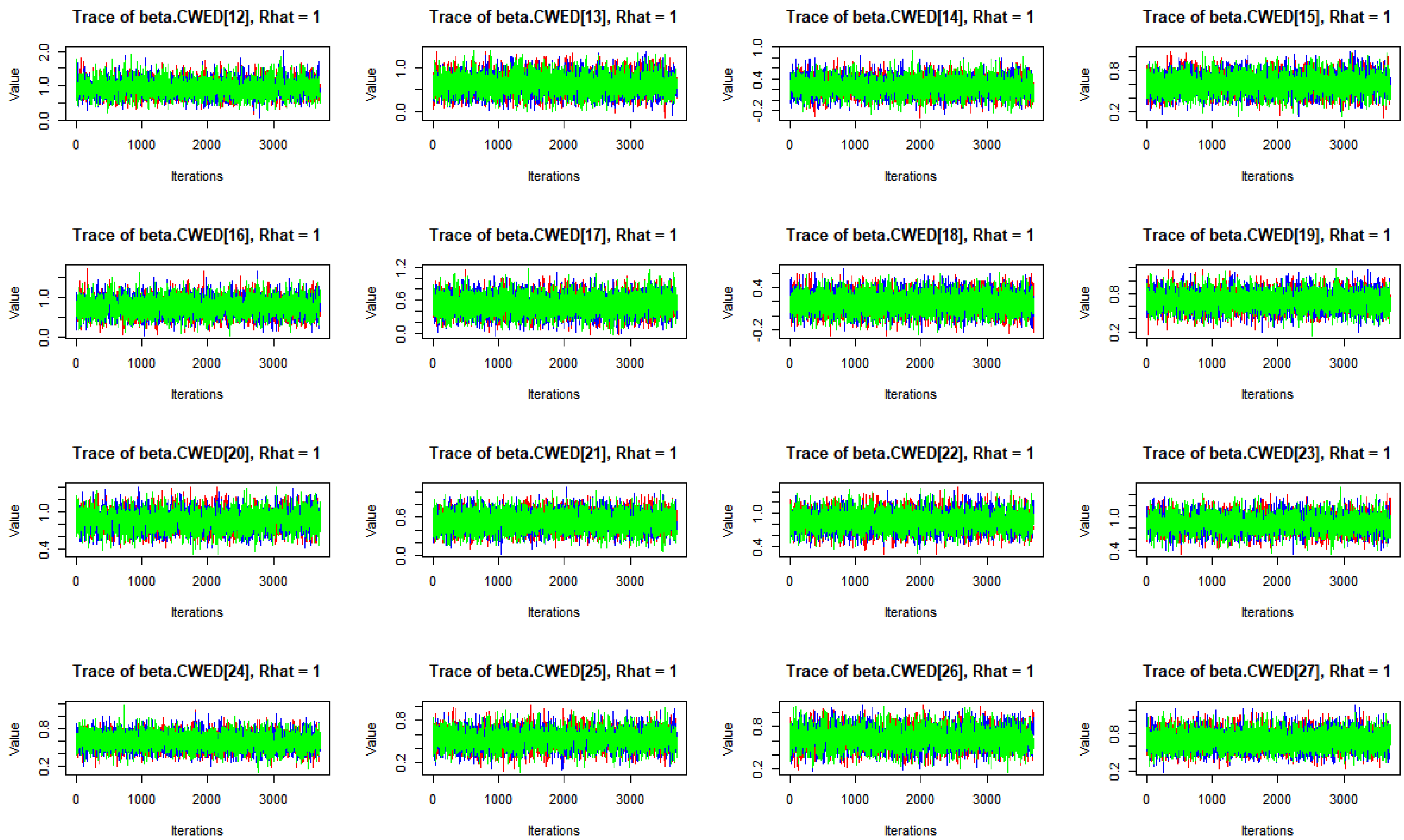

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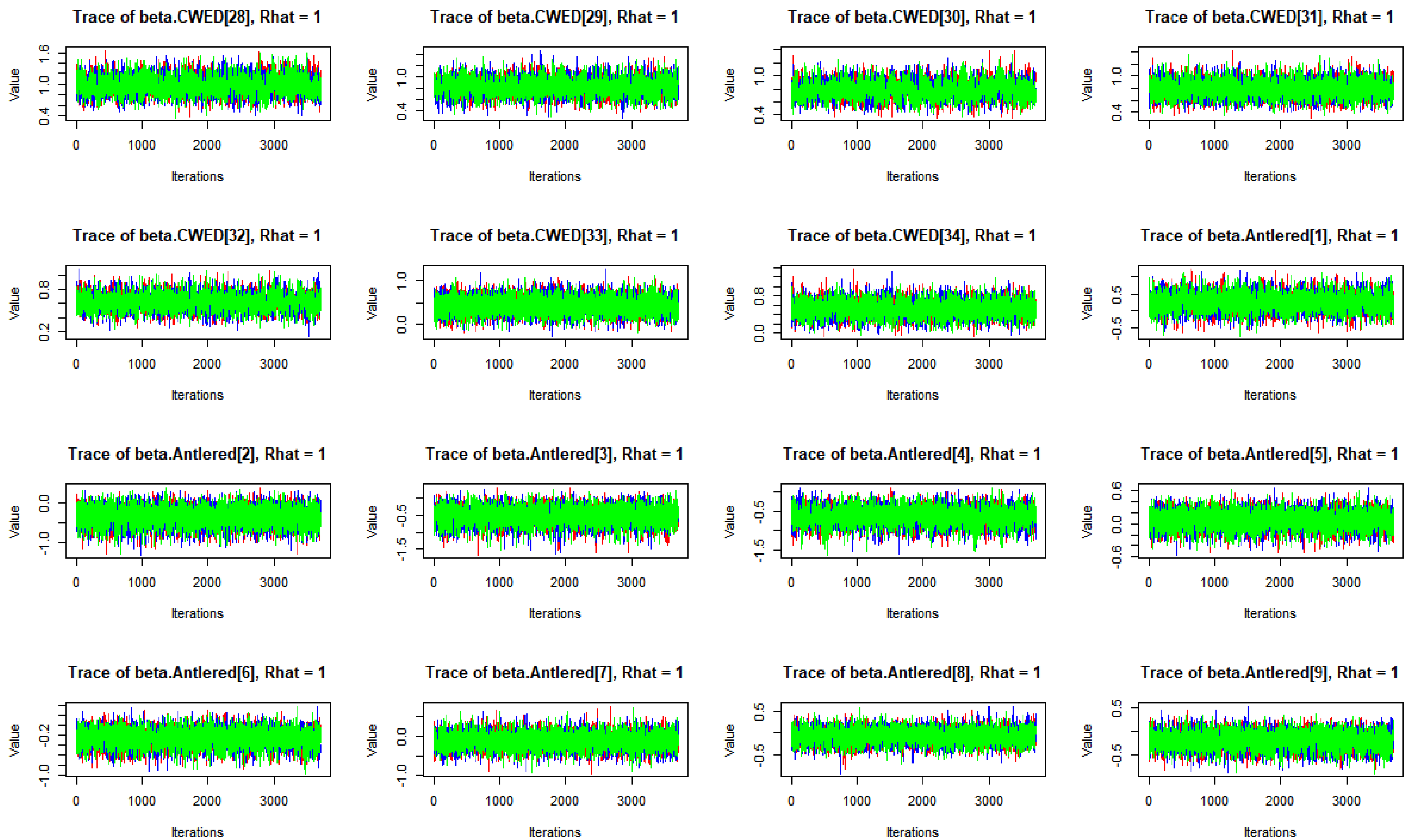

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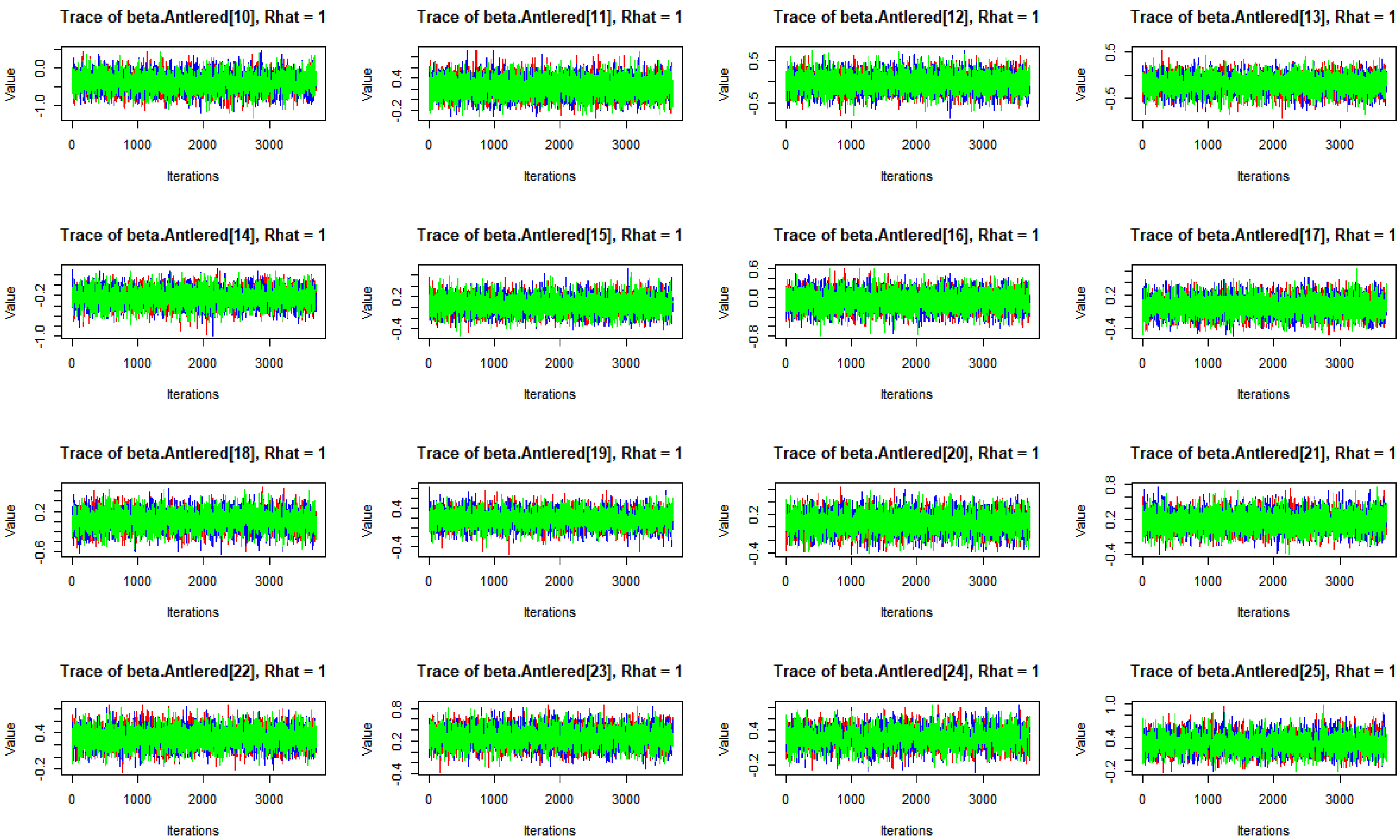

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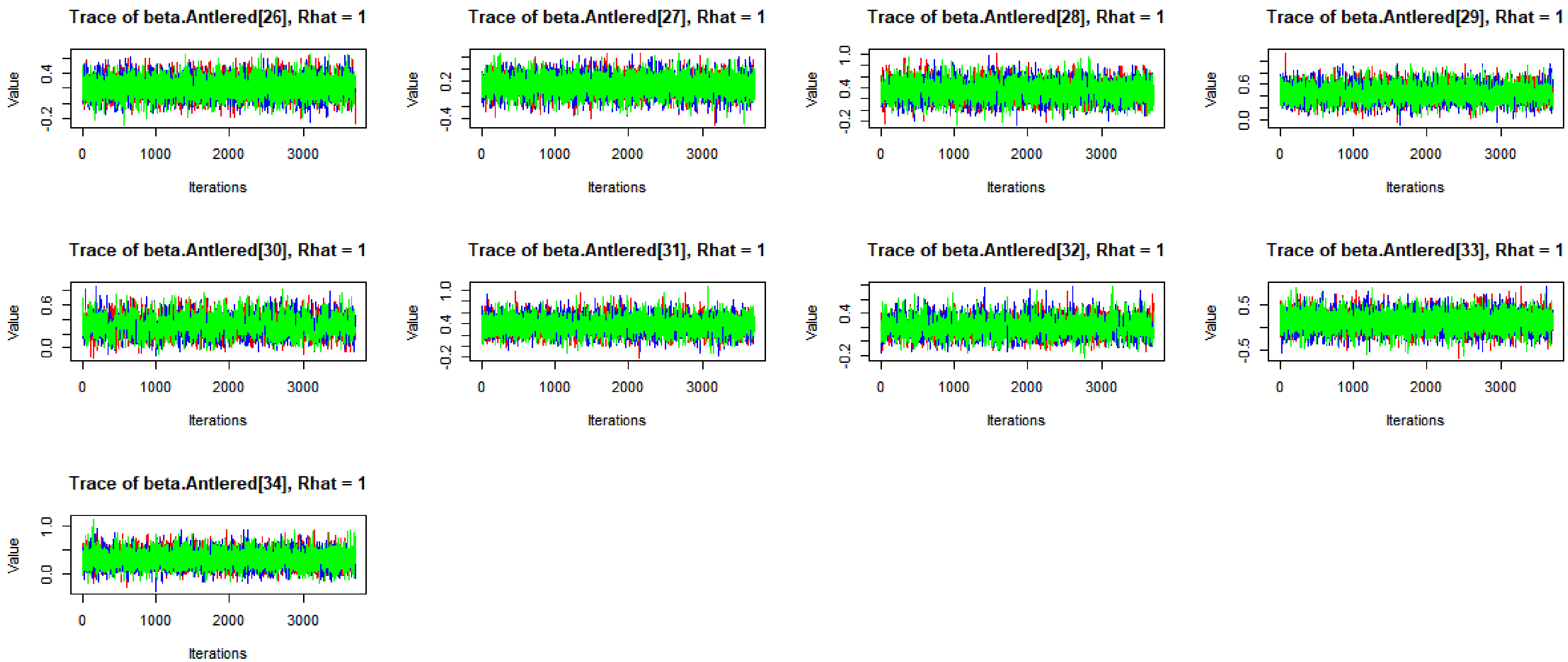

APPENDIX C: MAP OF ECOREGION CLASSIFICATIONS FOR COUNTIES IN WISCONSIN

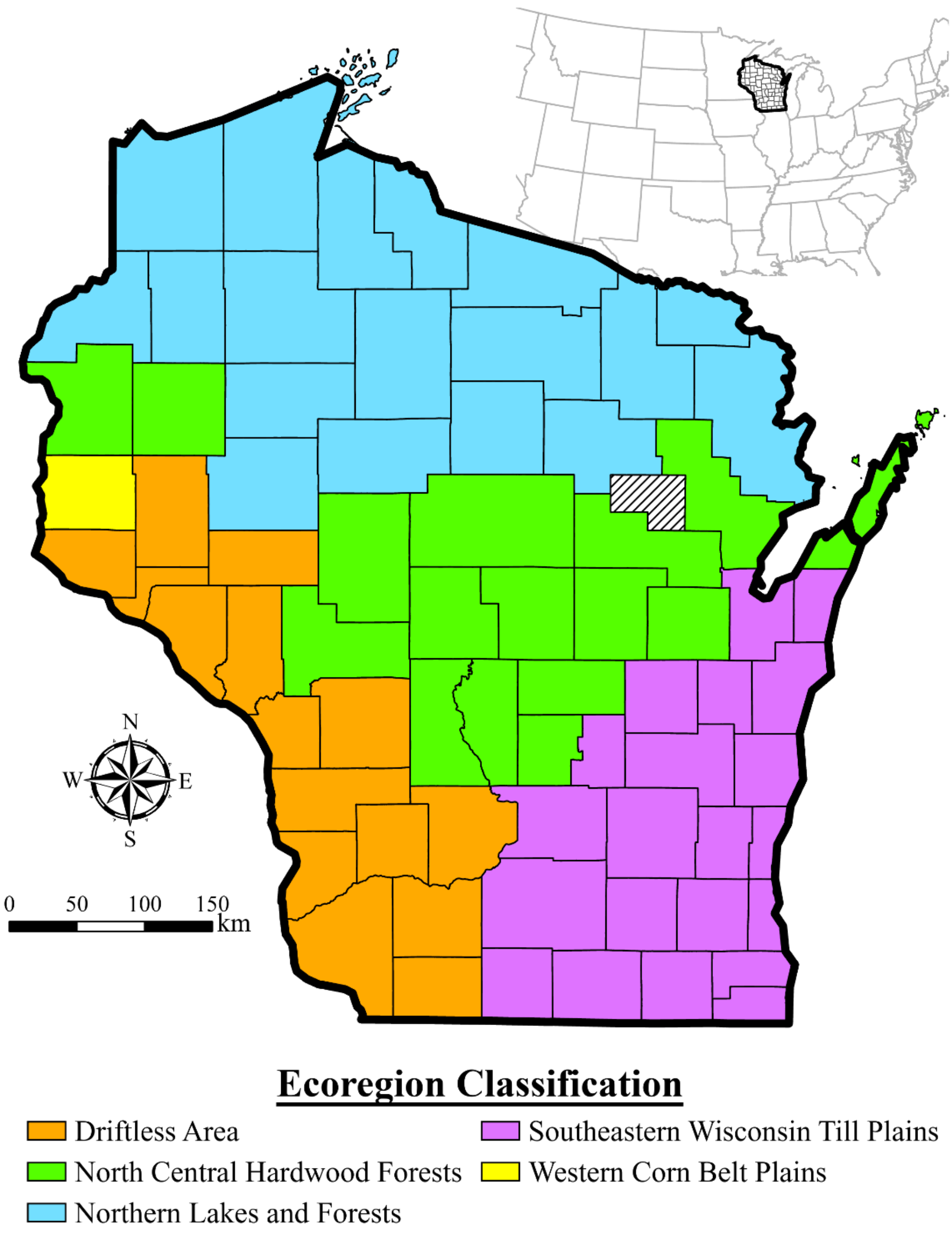

Figure 4.9 Map of ecoregion classification for each county in study area (Omernik 1987, Bailey 1995). I assigned an ecoregion to each county by determining which ecoregion covered the majority area within the county.

APPENDIX D: DIAGRAM OF PROCESS GENERATING RECORDS DATA

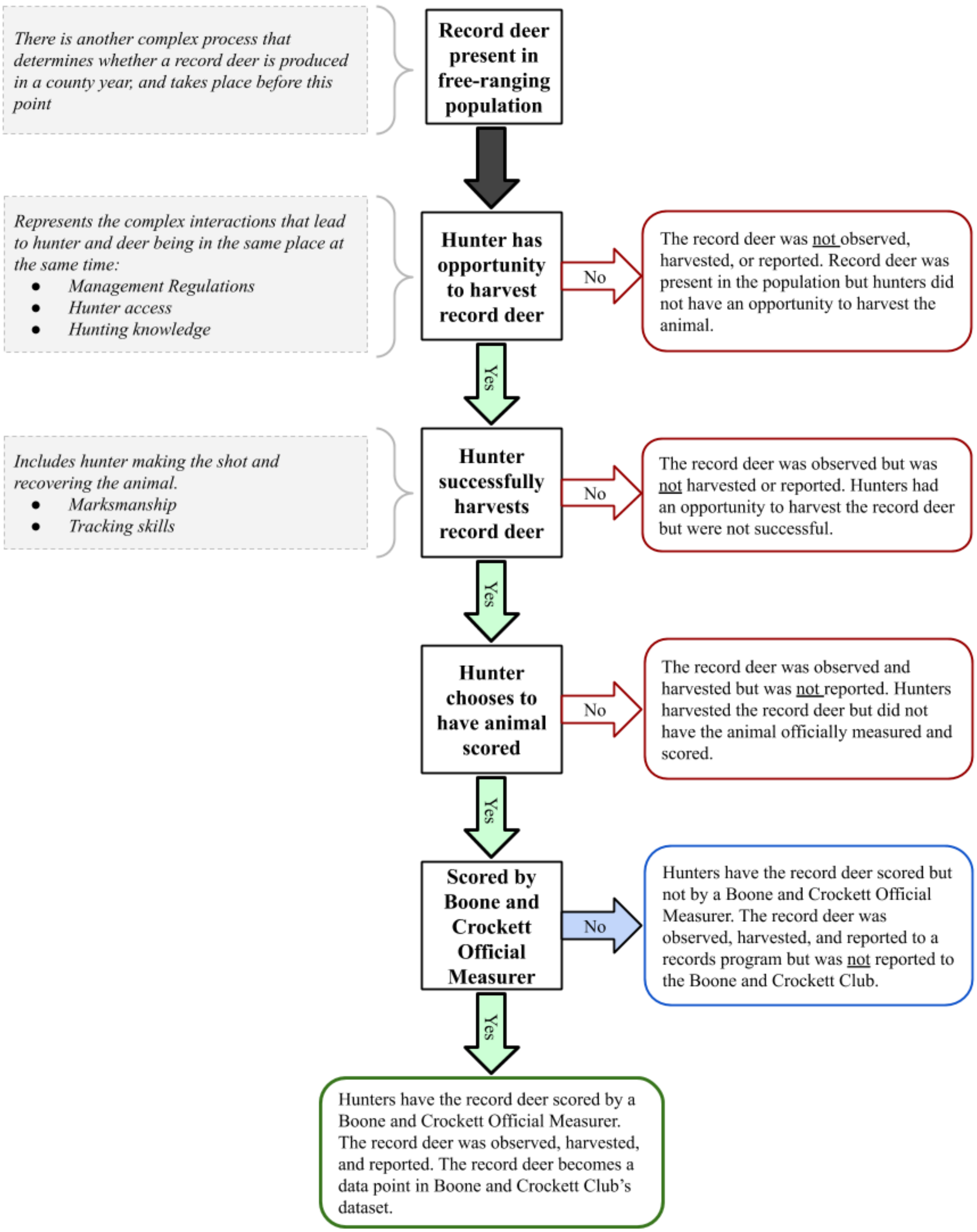

Figure 4.10 Infographic to show the sequence of critical steps required for a male white-tailed deer that has record-sized antlers to become a data point in the Boone and Crockett Club's Records of North American Big Game. Influential factors that may direct the outcome (Yes/No) of each step are given in the gray boxes.

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EPILOGUE

In my dissertation, I sought to test hypothesized outcomes of antler point restrictions, evaluate spatially explicit trends in antler sizes of record deer, investigate the relationship between management and record deer harvests, and apply modeling framework to account for imperfect detection and assess trends in record deer harvests. By analyzing trends in longitudinal harvest data and effects of environmental, management, and spatial contexts, this dissertation has shown how harvest outcomes relate to characteristics and regulations of the area. In this final section of my dissertation, I briefly review the findings and contributions from each chapter and suggest relevant research for future study.

Chapter 1 sought to determine whether antler point restrictions brought about changes in the age structure of the male harvest, antlerless harvest, or number of hunters when implemented in Michigan, USA. Antler point restrictions are designed to protect the majority of yearling males from harvest (Hamilton et al. 1995). In areas where antler point restrictions were implemented the proportion of yearling harvests decreased and greater proportion of the males harvested were from older age classes. However, antler point restrictions did not appear to cause a significant or lasting change in antlerless harvest or the number of hunters. The findings from this chapter can be used to help managers and hunters alike set reasonable expectations for changes in harvest outcomes under antler point restrictions.

Chapter 2 sought to evaluate the spatially explicit trends in antler sizes of record deer across the Midwest United States. The findings from this chapter underscored the importance of considering the spatial context when analyzing trends across large geographic areas. Accounting for space is important because global trajectories may not reflect trends happening at smaller spatial scales. For example, declining trends in antler sizes of deer across all records in North America (Monteith et al. 2013) versus the increasing trends in antler sizes of record deer in the Midwestern United States. The findings from this chapter also demonstrated that the spatial clustering of similar antler sizes through time is related to the ecoregion context rather than a management context. Managers may find the results from this chapter useful when communicating with hunters or landowners about their expectations for the deer in the area. Moreover, because the differences in average antler sizes followed ecologically delineated boundaries, rather than political boundaries, future studies using record deer might consider including these measures of ecological patterns and processes.

Chapter 3 sought to evaluate the degree to which management regulations influenced the harvest of record deer in the Midwest United States and review evidence for spatial and temporal biases in reporting. Although some ecoregions seem to have inherently more record entries than others, management regulations do appear to have some influence on the harvest of record deer. In areas of highly suitable habitat for white-tailed deer, management regulations, such as shorter season and limiting the harvest of antler deer, can provide enhancements to survival of antlered deer that may result in the additional harvest of record deer.

Chapter 4 sought to incorporate detectability in the modeling framework to make inferences about the harvest of record deer. In this chapter, I demonstrated the applicability of the N-mixture modeling framework (Royle 2004) to evaluate harvests of record deer in Wisconsin. The results suggest that reporting rates vary randomly across space and do not follow any obvious temporal trends. Analyzing harvest data under the N-mixture modeling framework may also provide new opportunities to understand the functional relationships between deer harvests and environmental covariates.

As interest in quality deer management and harvesting adult males with large antlers increases (Connelly et al. 2012, Harper et al. 2012), it is important for wildlife managers and hunters to understand how regulations and habitat can influence harvests of record deer. Further research is needed to determine the causes of imperfect detection, including information on existing barriers in reporting record harvests and factors affecting the probability that a hunter reports a record deer. Addressing the need for information related to imperfect detection will require studies in human dimensions and hunter behaviors.

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